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A Morphological and Phylogenetic Examination of the Miocene and Pliocene Bivalve Genus Chesapecten

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A Morphological and Phylogenetic Examination of the Miocene and Pliocene Bivalve Genus *Chesapecten*

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by

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Abstract

The scallop genus *Chesapecten*, characterized by its strong ribbing and large size, originated in the early Miocene and was extinct by the late Pliocene. It was highly abundant in the mid Atlantic region of the U.S. and an important component of marine ecosystems. The genus is comprised of nine species and is widely thought to represent an example of gradual evolution. The limited geographic and stratigraphic ranges of each species make them important indicators for the Coastal Plain deposits in which they are found. However, because of high variability within species and hybridization between species, they can be difficult to identify based solely on morphology.

This study quantitatively defined the species of *Chesapecten* through: (1) a morphological assessment of late Miocene and early Pliocene species, (2) an examination of genus-wide trends in morphology through time, and (3) a phylogeny of the genus. Specimens for the morphological assessment were collected from Cobham Wharf (Surry County, Virginia) and included all three species present at that location (*C. middlesexensis, C. jeffersonius, C. madisonius*), while those used for the phylogeny were obtained from the collections at the Virginia Museum of Natural History (Martinsville, Virginia) and included eight defined species. A portion of the cliff at Cobham Wharf was bulk-sampled at half-meter increments, yielding seven total samples with about 12 specimens each. Approximately 96 museum specimens were selected for the analysis.

Analyses involved collecting 10 morphologic landmarks defining shell shape from each field specimen and approximately 40 discrete and continuous characters describing shell shape and ornamentation from each museum specimen. Landmark data were Procrustes transformed to eliminate variation based on size, rotation, and location. From this, principal components analysis was used to produce a morphospace.

Phylogenetic data were used to reconstruct a parsimony-based phylogeny and bootstrapping allowed us to assess overall robustness of tree topology. Morphological results indicate that some features display trends through time and can be used to distinguish species. Phylogenetic results produced an evolutionary sequence that differs from the stratigraphic sequence, suggesting a more complex explanation of the evolutionary history of *Chesapecten* than anagenesis.

Introduction

The scallop genus *Chesapecten* is locally highly abundant (Shapiro 1981) in mid-Atlantic Miocene and Pliocene deposits and is an important stratigraphic indicator for units in this region (Ward and Blackwelder 1980). Its high abundance indicates that it was a major component of the marine ecosystem in which it lived, and it is thus important in paleoenvironmental studies of the mid-Atlantic Neogene.

Ward and Blackwelder (1975) described species within the genus based on a series of morphological traits. Other studies (Shapiro 1981; Miyazaki and Mickevich 1982; Kelley 1983) have more closely examined the morphology and phylogeny of the genus, but none have provided a complete quantitative analysis. Through this research, I seek to quantitatively assess the currently accepted species definitions and evolutionary relationships within this genus by asking the following questions:

- What morphological traits can be used to distinguish *Chesapecten middlesexensis* and *Chesapecten jeffersonius*?
- How does morphology of *Chesapecten* species change through time?
- What are the phylogenetic relationships among *Chesapecten* species?

A quantitative understanding of both the morphology and phylogeny of *Chesapecten* is important to field-based studies of the mid-Atlantic stratigraphy. *Chesapecten jeffersonius*, in particular, is an index fossil for identifying the Sunken Meadow Member of the Yorktown Formation (Ward and Blackwelder 1980); however, especially when in the field, it is often difficult to differentiate it from *C. middlesexensis*. A more concrete morphospecies definition will aid in the identification of all species of *Chesapecten*. Additionally, the genus is widely accepted as an example of gradual microevolution (Prothero 2007); however, a well-crafted phylogeny does not yet exist. By generating one through quantitative methods, I aim to better explain the commonly accepted evolutionary patterns.

Background

Chesapecten

The genus *Chesapecten* is classified under the phylum Mollusca, class Bivalvia, order Pectinoida, family Pectinidae (Paleobiology Database 2011). It originated in the early Miocene and went extinct by the late Pliocene (Ward, pers. comm. 2010) and occurs predominately in the mid-Atlantic region of North America (figure 1).

Figure 1: Geographic distribution of *Chesapecten*
Chesapecten lived in the mid-Atlantic region of North America (Paleobiology Database, 2011).

Species of *Chesapecten* were a part of the benthic shallow marine community and were likely epifaunal suspension feeders (Paleobiology Database 2011). Some species had limited swimming capabilities, which was likely a function of adductor muscle location (Miyazaki 1978) as well as general shell size and shape (Shumway and Parsons 2006). Variation in other shell features such as byssal notch, ornamentation, convexity, and the amount of space between each valve when closed also allowed for the evolution of free-swimming ability in some species (Stanley 1972).

Chesapecten shells are fan-shaped with dorsal auricles and contain a variable number of ribs (figure 2). Individual size varies; across most species the average adult has a maximum length of approximately 10 cm, but in some species, the largest adults can be as small as 5 cm and as large as 16 cm. Juveniles are much smaller, with maximum lengths of less than 2-3 cm. Each individual has a left and right valve, which are distinguished by the location of the byssal notch and adductor muscle scar.

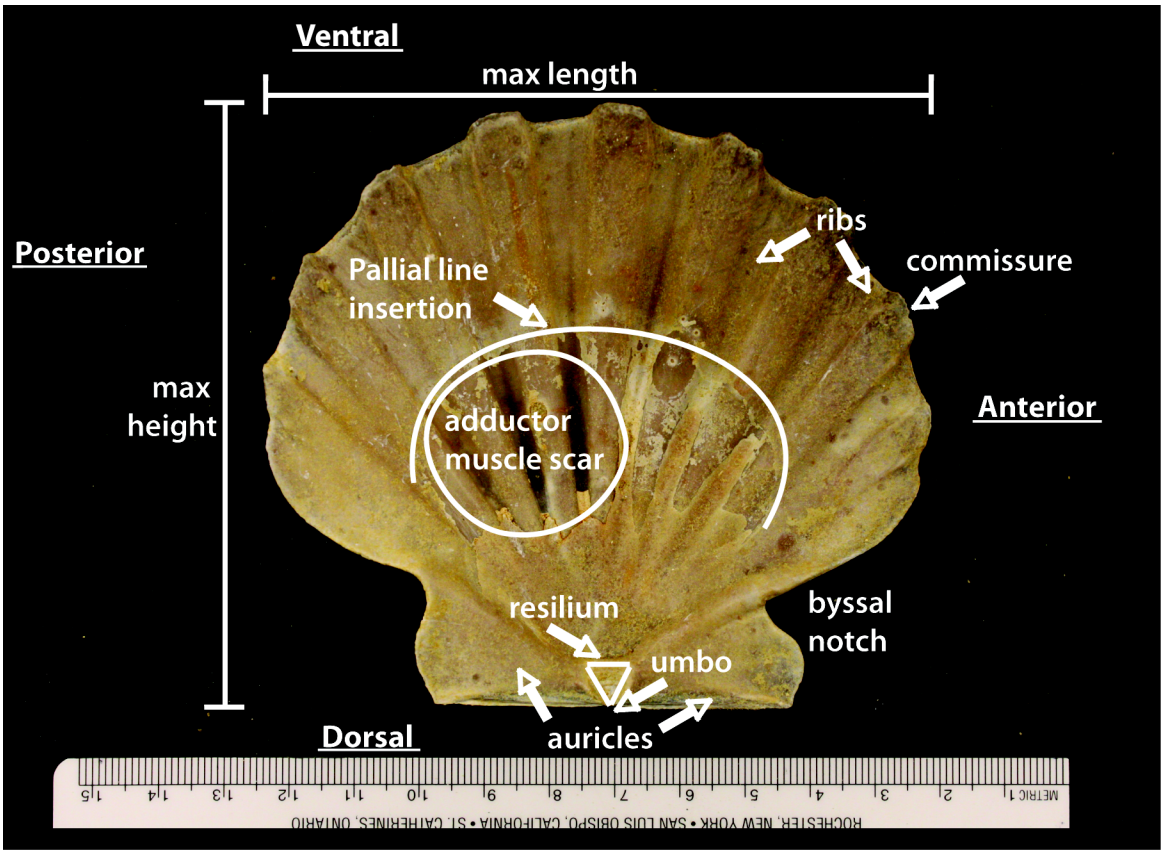

Figure 2: Shell morphology
The image identifies anatomical features of *Chesapecten*.

Ward and Blackwelder (1975) first described seven of the species of *Chesapecten* and distinguished them from other scallops based predominantly on their large size, strong ribbing, and scaly ornamentation. The total number of species in the genus is uncertain, as there is debate over the existence of intermediate morphs and location-specific varieties that are based on only a few specimens. This study focuses on the eight species that can easily be collected in reasonably sized samples.

Stratigraphically, *Chesapecten* occur in formations within the Chesapeake Group (figure 3). Because, with few exceptions, each species neatly coincides with a particular formation or member, this stratigraphic sequence is considered to represent the gradual

microevolution of the genus (Prothero 2007). Exceptions to the one species per stratigraphic layer pattern are that *C. nefrens* is in two units and that *C. madisonius* and *C. middlesexensis* are in the same unit. Miyazaki (1978) described how the evolution of *Chesapecten* relates to changes in ontogenetic development in the form of paramorphosis, in which the adults of ancestral species resemble only the juveniles of derived species and adults of derived species are more developed.

The extinction of *Chesapecten* coincides with the Pliocene-Pleistocene extinction, during which there was an overall loss in diversity of Pectinidae (Smith and Jackson 2009). This extinction has been linked to changes in oceanographic conditions that resulted from the formation of the Isthmus of Panama and the subsequent separation of the Atlantic and Pacific oceans (Stanley 1986).

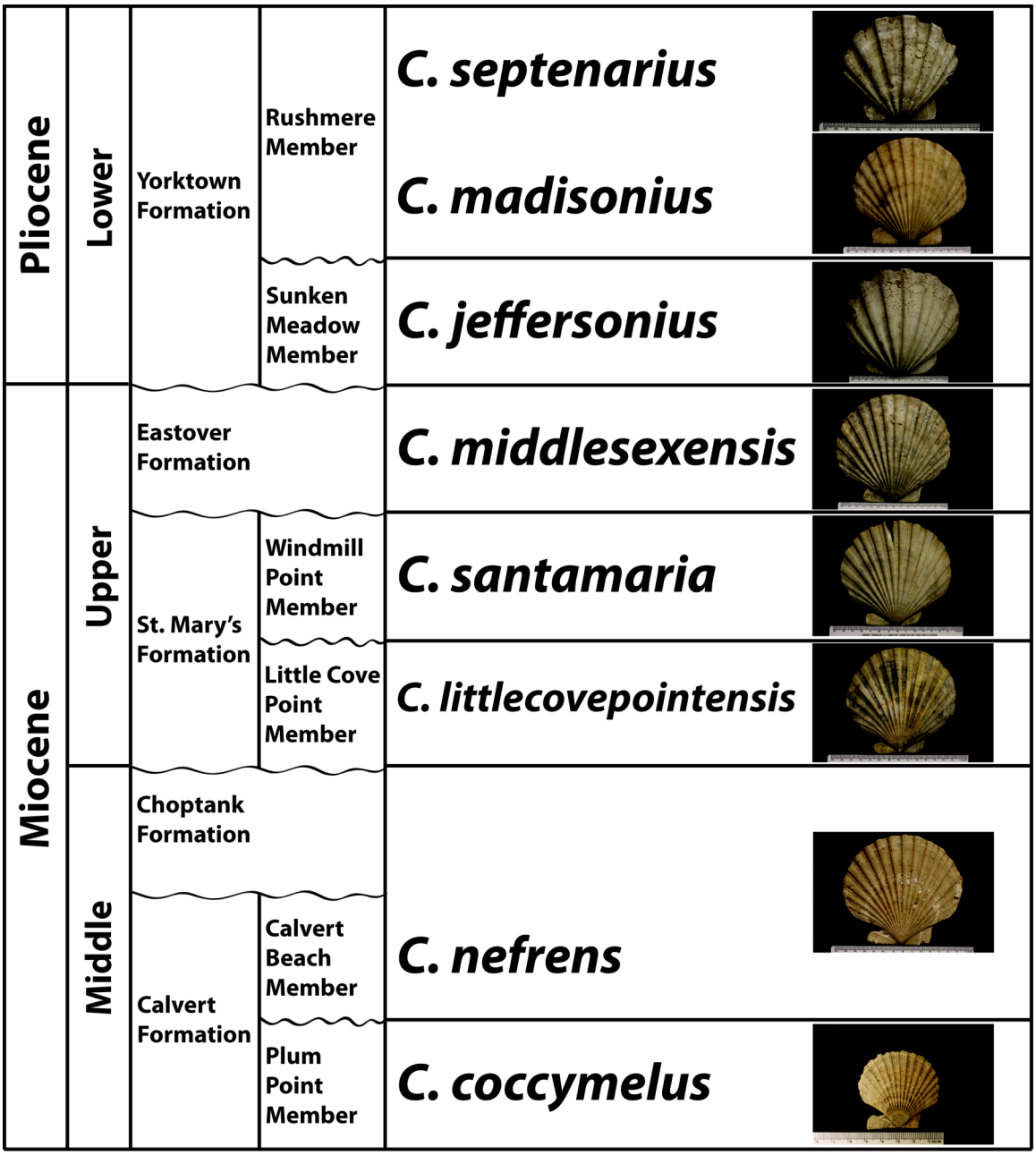

Figure 3: Stratigraphic sequence of *Chesapecten*
Species are stratigraphically correlated with the formations of the Chesapeake Group. Except for *C. nefrens,* which is in two units and *C. madisonius* and *C. septenarius,* which are in the same unit, there is a one-to-one relationship between species and stratigraphic units. Images representing each species highlight subtle changes in morphological features, such as overall shape and rib number, that occurred within the genus from the middle Miocene to lower Pliocene. This sequence represents about 30 million years of time (modified from Ward & Blackwelder 1975; Ward 1992; Johnson et al. 2001).

Geologic setting

All species of *Chesapecten* are found in the Calvert, Choptank, St. Mary's, Eastover, and Yorktown Formations of the Chesapeake Group (Ward 1992). These formations, which contain shelly sands and clays, range in age from lower Miocene to upper Pliocene and are geographically located in Maryland and Virginia (Ward 2008). Each formation represents a transgressive sequence of Coastal Plain sediments. Each sedimentary unit was deposited during a sea level high stand, and there are unconformities between each unit that represent times of sea level low stands. The depositional environment was a shallow marine, near-shore environment. The presence of glauconite suggests open ocean conditions.

Methods

Field sample collection

Samples were collected from an outcrop exposed along the cliffs at Cobham Wharf, located along the James River in Surry County, Virginia (figure 4). The sampling location was chosen based on accessibility and completeness of the stratigraphic section. The portion of the cliff that was selected contained a full exposure of the Eastover Formation and both the Sunken Meadow and Rushmere Members of the Yorktown Formation. Seven bulk samples were collected up the face of the chosen section of cliff at intervals of 0.5 meters (figure 5).

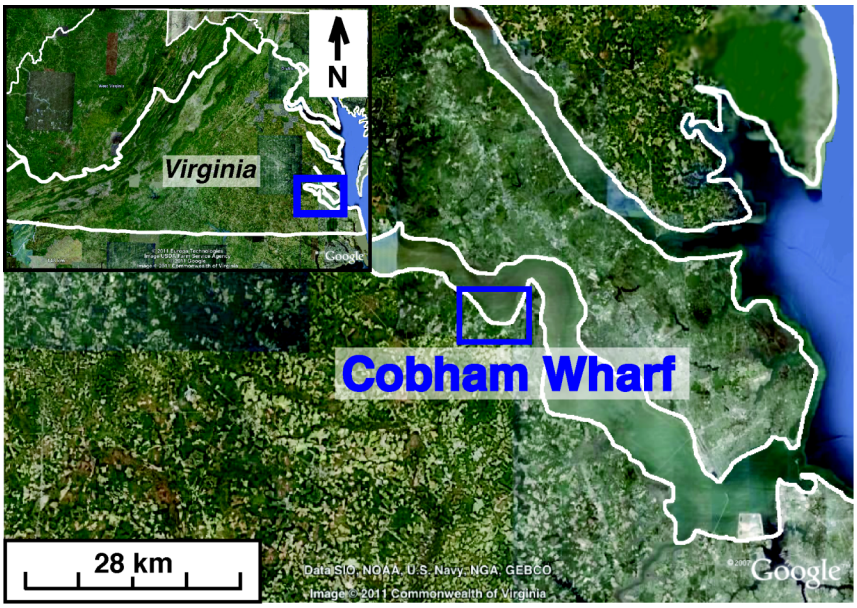

Figure 4: Map of Cobham Wharf
Field samples were collected from the cliffs at Cobham Wharf, which is located along the James River in Surry County, Virginia.

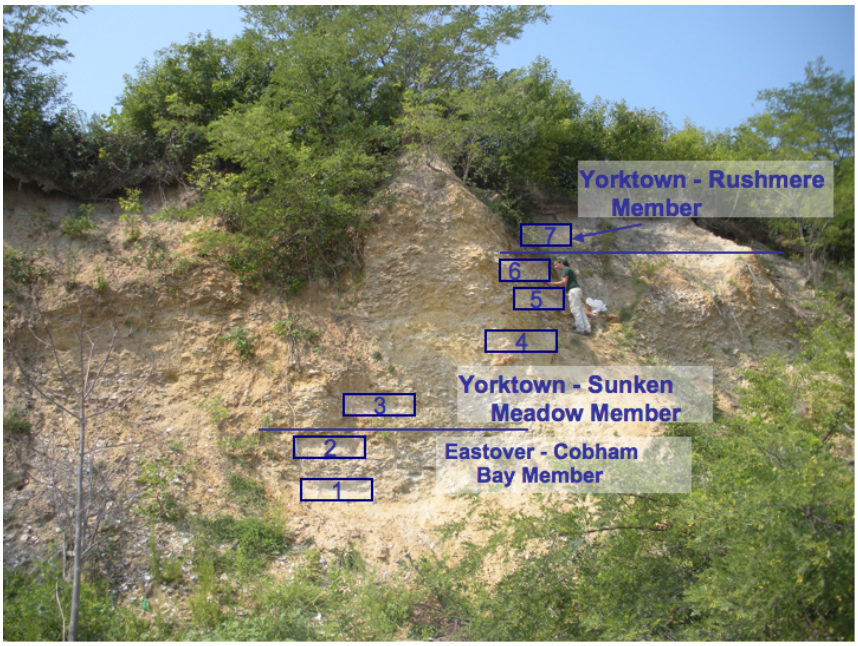

Figure 5: Location of field samples
Samples were collected at 0.5 m increments from all visible formations. The boundary between the Eastover and Yorktown Formations lies between samples 2 and 3. The boundary between the Sunken Meadow and Rushmere Members of the Yorktown falls between samples 6 and 7. Both of these boundaries are erosive unconformities. Only samples 1-6 were included in the analysis.

Each sample included *Chesapecten* and associated sediment. Dimensions of the bulk sample varied in order to obtain approximately 12 specimens where possible. For sample locations higher up the cliff, it was physically difficult to remove complete specimens and transport them down the cliff intact, so some contain fewer than 12 specimens. Large individuals, those greater than 5 centimeters, were preferentially selected to minimize ontogenetic variation. Sediment in each sample varied slightly but on average was medium to fine grained sub-angular sand composed of greater than 90% quartz and a small percentage of glauconite. All samples were highly fossiliferous. Complete sedimentological descriptions of each sample can be found in Appendix A. The Rushmere Member was slightly cemented, making sample collection very difficult. In the process of specimen preparation, sample 7, the only sample from the Rushmere Member, was removed from the study because it was impossible to remove the cemented sediment from the specimens.

Landmark collection

Landmark coordinates were collected from photographs of right and left valves of *Chesapecten* specimens collected in the field. Photographs were taken of the internal features of the shells with each individual arranged in the same orientation in order to minimize variability of landmark location among individuals. Additionally, the effect of ontogenetic changes on morphology was minimized through the exclusion of juvenile individuals from the study. Miyazaki (1978) considered juveniles to be individuals that measure less than about 3 centimeters in height. However, since bivalves exhibit indeterminate growth, it is difficult to concretely differentiate juveniles from adults, so in

order to further eliminate any ontogenetic variation, the largest individuals possible were selected and individuals smaller than 5 centimeters were not photographed.

Landmark data points were collected using tpsDIG software, which created a digital point at the location of 10 homologous and pseudo-homologous landmarks (figure 6). Homologous landmarks, such as those that define the auricle region, were preferred because the location is a consistently identifiable point on all individuals. However, since the commissure of the shell does not include homologous landmarks, pseudo-homologous landmarks were used to define the maximum height and length. The maximum height was defined by points through which a line can be connected that is perpendicular to the hinge and bisects the shell. The maximum length was defined as the most anterior and most posterior points through which a line parallel to the hinge can pass. In order to account for poor preservation of many of the shells, for every specimen, each landmark was assigned a confidence ranking based on completeness of the shell outline. Confidence varied from high, medium, and low depending on the amount of shell material present and the predictability of shell outline. Landmarks with low confidence that could be identified as outliers to the data set were removed.

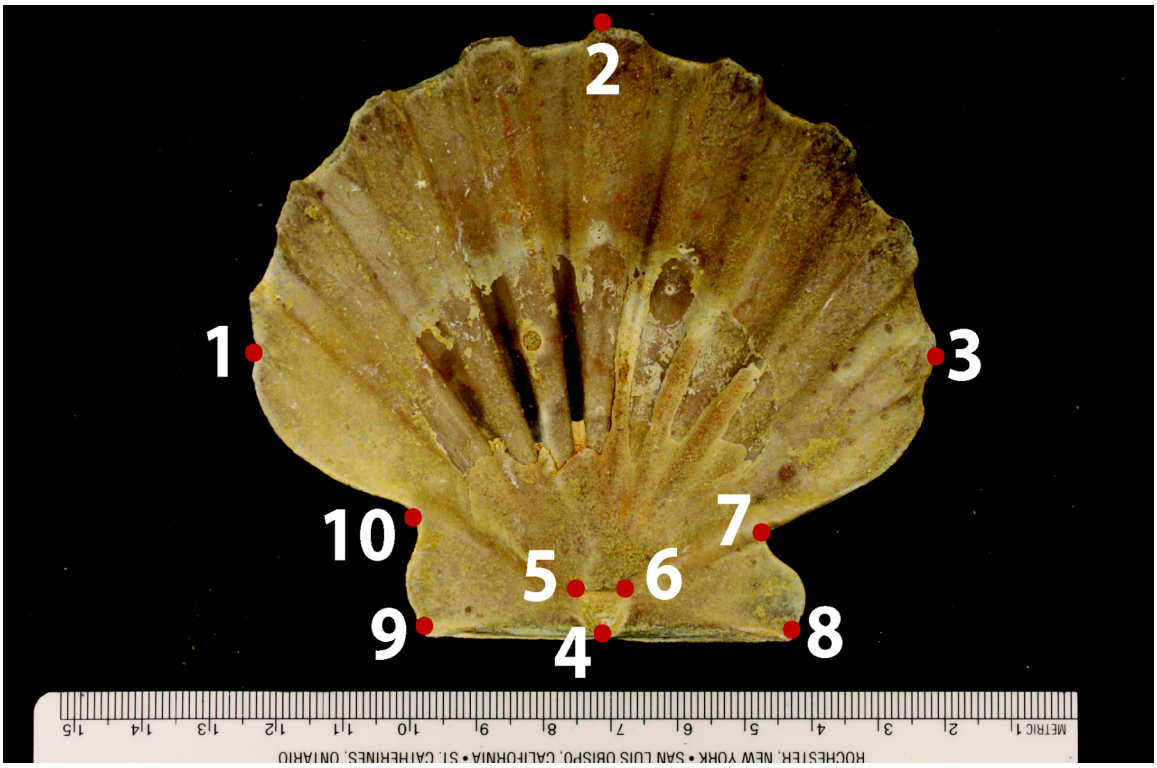

Figure 6: Landmark locations
Points indicate the location of 10 landmarks. Landmarks 1-3 are pseudo-homologous, and landmarks 4-10 are homologous.

A morphopace was created using the PAST software. Landmark coordinate data were imported to PAST and converted using a Procrustes transformation to eliminate variation based on size, orientation, and rotation. The Procrustes-transformed data were analyzed using principal components analysis, which simplifies the x and y coordinates for 10 landmarks into principal components that are ranked according to the extent to which they explain variation within the morphospace. Principal components 1 and 2, which explained almost 50% of the variation were graphed against each other to create the morphospace.

Museum sample collection

Samples from eight species of *Chesapecten* (*C. coccymelus, C. nefrens, C. santamaria, C. littlecovepointensis, C. middlesexensis, C. jeffersonius, C. madisonius,* and *C. septenarius*) were collected from the Virginia Museum of Natural History in Martinsville, Virginia. Specimens for each species were collected from both the type locality and a second locality, where available. When possible, six specimens were chosen, three right and three left valves, for each location. Large specimens, those greater than 5 centimeters, were preferentially selected to minimize ontogenetic variation.

Character state collection

Approximately 40 unordered characters, both discrete and continuous, were measured from right and left valves of museum specimens (Appendix B). These were developed from characters used in the literature (Ward and Blackwelder 1975; Miyazaki and Mickevich 1980; Smith 1991) to define species of *Chesapecten* and differentiate them from other scallops. These characters were imported into the TNT software in order to construct a phylogeny based on the most parsimonious arrangement. *C. coccymelus* was used as an outgroup since it is the earliest occurring species of those studied.

Results and Interpretation

Analysis of differences between C. middlesexensis and C. jeffersonius

In order to identify the extent to which the landmark coordinates can differentiate field specimens of *C. middlesexens* and *C. jeffersonius*, data were analyzed using principal components analysis and generating a morphospace. Results of the principal components analysis indicated that principal components 1 and 2 explain 48.022% of all variation in the samples (tables 1 and 2). Loadings for each of these principal components

indicate that most of the variation is due to landmarks 7, 8 and 3, which represent the shape of the byssal notch, anterior auricle, and anterior point of the maximum length (figures 7 and 8). Landmarks with higher loadings have a higher correlation between the x or y coordinate and the principal component in question. If the loading value is positive then the correlation between that coordinate and the principal component is positive, and if the loading is negative the correlation is also negative. The morphospace (figure 10) was created based on values for principal components 1 and 2.

PC	Eigenvalue	% Variance
1	0.0016643	29.021
2	0.00108968	19.001
3	0.000887645	15.478
4	0.00060434	10.538
5	0.000443957	7.7413
6	0.00030115	5.2512
7	0.000253456	4.4195
8	0.000137713	2.4013
9	0.000103597	1.8064
10	9.59E-05	1.6717
11	6.19E-05	1.08
12	3.73E-05	0.6499
13	2.37E-05	0.41412
14	1.58E-05	0.27632
15	8.15E-06	0.14211
16	5.23E-06	0.091135
17	1.00E-06	0.017462
18	5.40E-16	9.42E-12
19	4.09E-16	7.13E-12
20	2.30E-16	4.01E-12

Table 1: Eigenvalues for principal component analysis

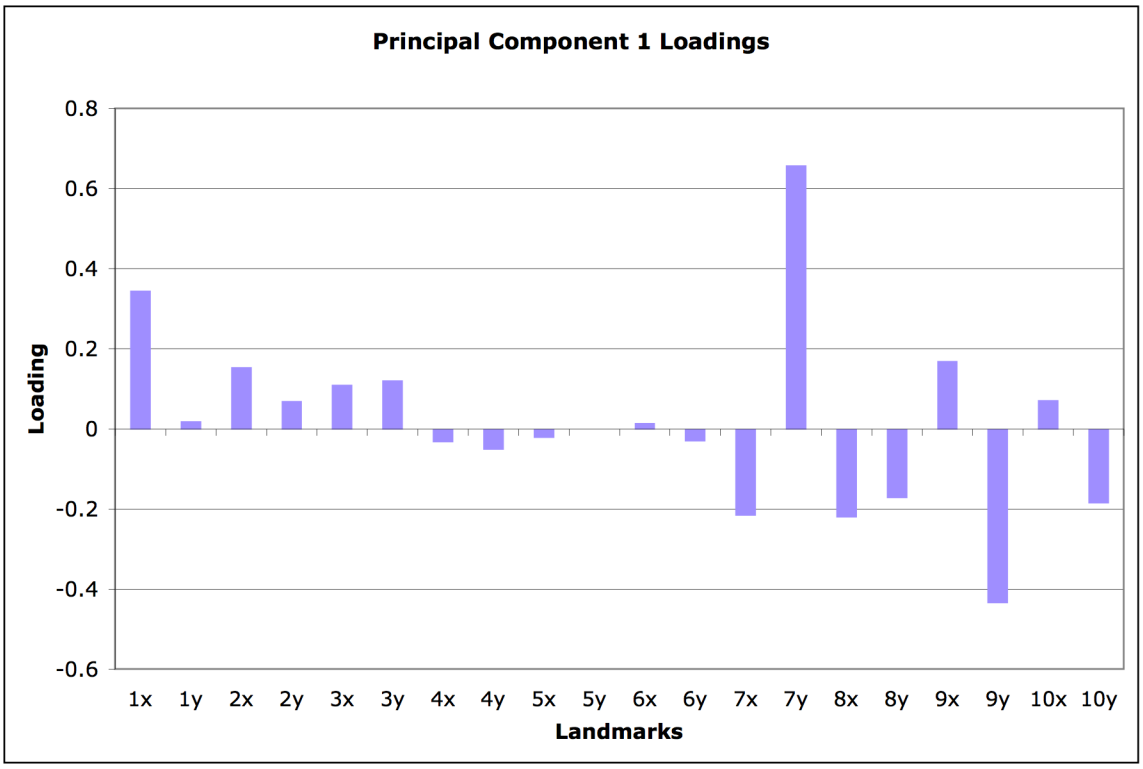

Figure 7: Principal component 1 loading values
Landmark 7y is responsible for the majority of the variation in principal component 1. Since the loading value for this coordinate is positive, it increases as principal component 1 increases.

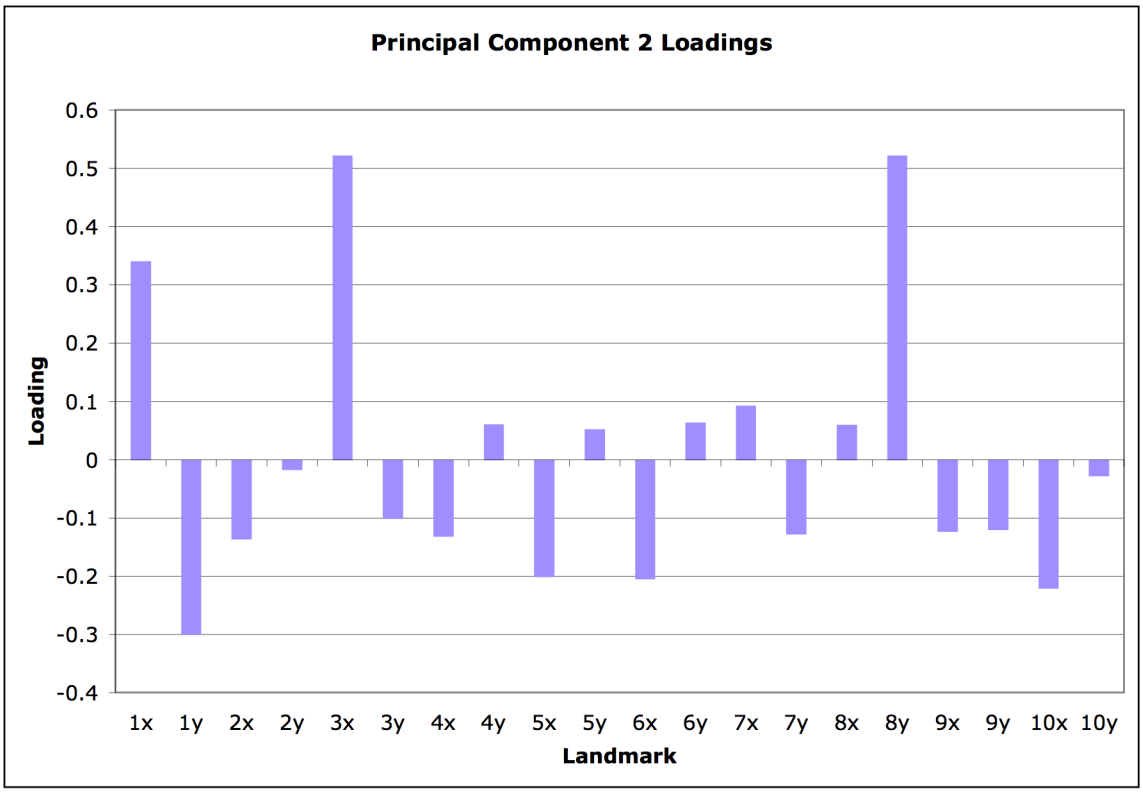

Figure 8: Principal component 2 loading values
Most of the variation in principal component 2 is the result of landmarks 3x and 8y. Both of these coordinates have positive loading values so they have a direct relationship with the value of principal component 2.

From the loading analysis, it is possible to understand how landmark coordinates shift with an increase or decrease in principal component values (figure 9). For example, landmark 7y, which has a positive loading value, increases as principal component 1 increases. This means that the coordinate point will move up along the y-axis. In contrast, since landmark 7x has a negative loading, it will decrease with an increase in principal component 1, so the coordinate will move to the left along the x-axis.

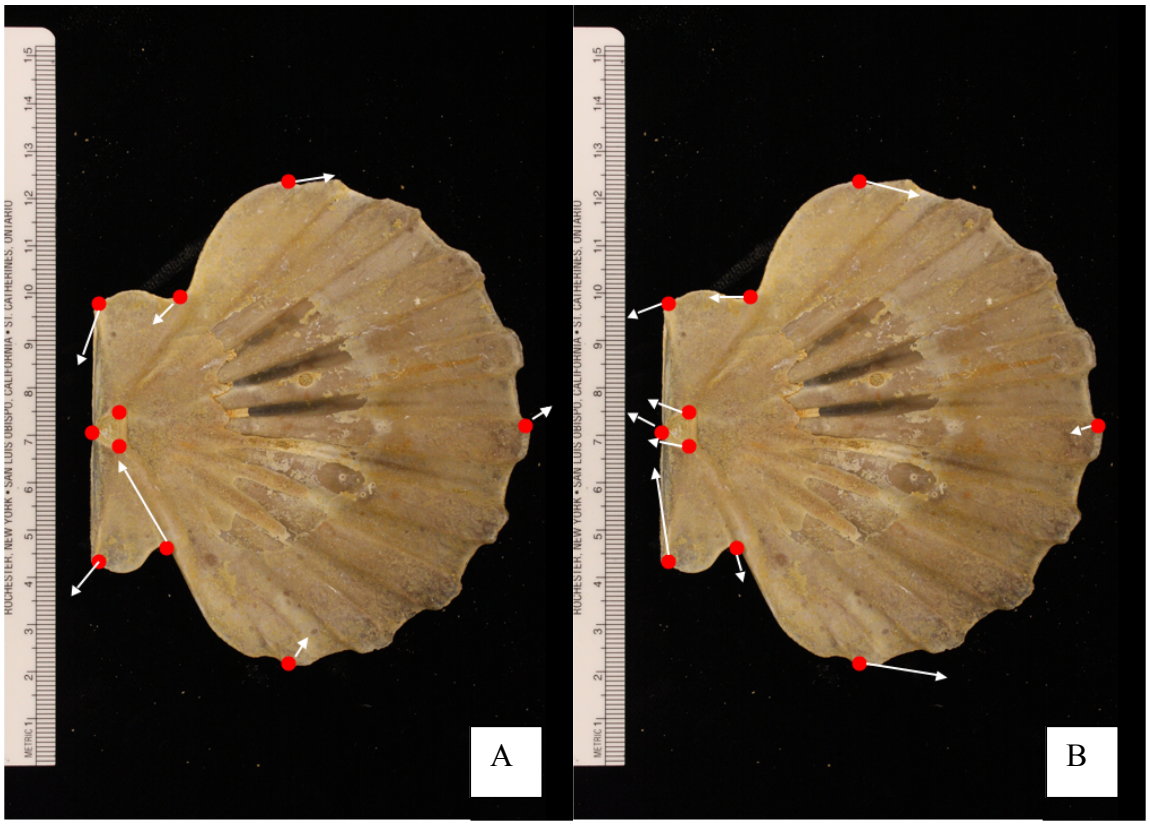

Figure 9: Relationship between principal component values and morphology
As principal components 1 (A) and 2 (B) increase, the morphology of *Chesapecten* shells changes based on loading values for each landmark coordinate. Red dots represent the ten landmark locations and the arrows indicate direction of principal component value increase. Coordinates with positive loading values increase along the x- or y-axis, while those with negative loading values decrease along the x- or y-axis.

There is significant overlap between where each of the samples plots in morphological space (figure 10), suggesting that variation within samples is similar in magnitude to variation between samples. This overlap is especially prevalent in figure 11 where points on the morphospace are shaded based on expected species. When examining the morphospace based on the accepted species definitions, it is easy to see that variation within *C. middlesexensis* and *C. jeffersonius* is great and that the distinction between the two species is not clear. This means that field specimens of these two species

cannot be distinguished based on morphological shape alone. There are, however, regions of the morphospace that are not occupied by certain samples, which indicates some distinction between samples despite the overall lack of distinction between species. This could be due to environmental differences or hybridization of species.

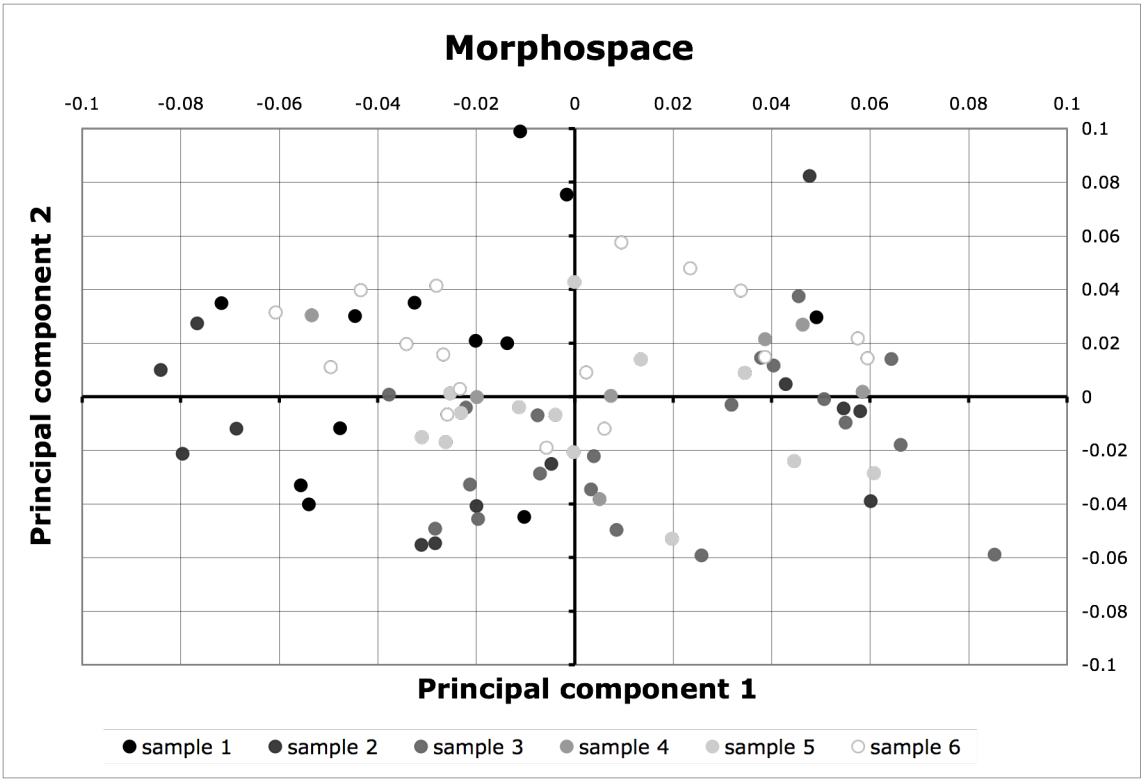

Figure 10: Morphospace categorized by sample
Principal components 1 and 2 are graphed against each other to generate a morphospace. Each point represents an individual specimen and points are graded according to the six samples.

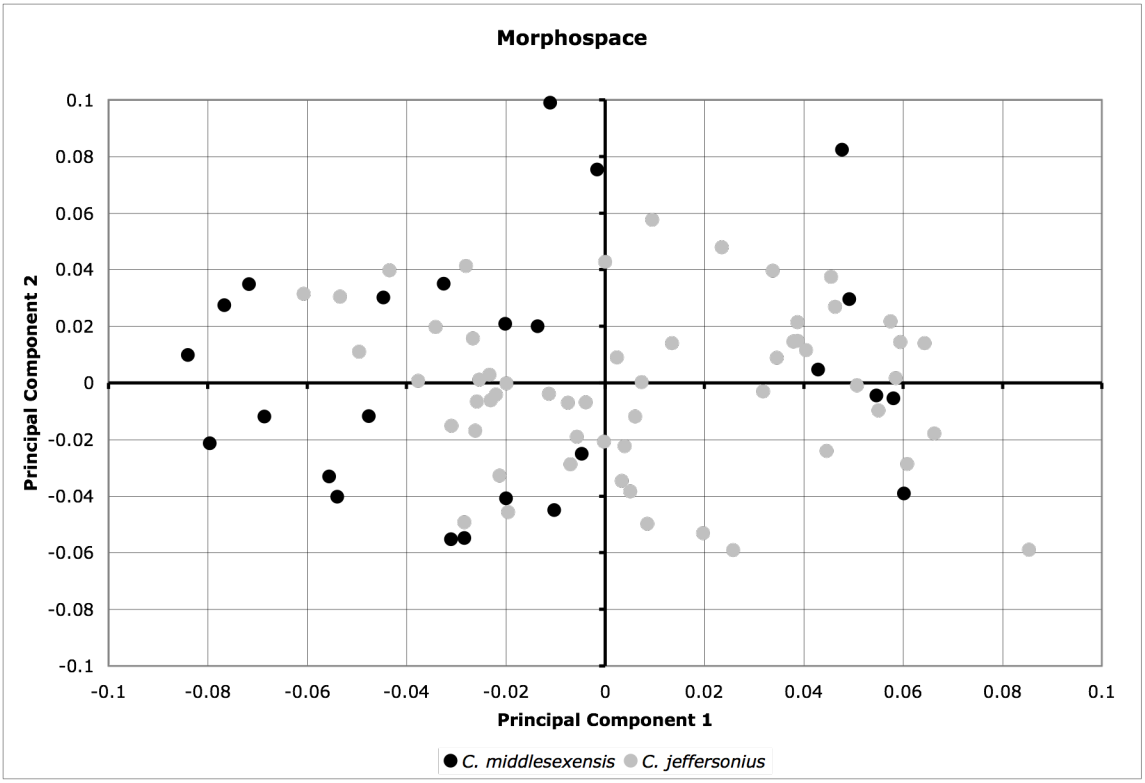

Figure 11: Morphospace categorized by species
Same morphospace as figure 10, but each point, which represents an individual specimen is coded based on expected species. There is significant overlap between the two species.

Differences between samples are reflected in the significant difference (as determined by an ANOVA with Tukey test) between the means of the principal component 1 values ($F_5 = 2.339$, $p = 0.05$) for samples 1 and 3 (Tukey test, $p = 0.028$) and the means of principal component 2 values ($F_5 = 4.096$, $p = 0.002$) for samples 1 and 3 (Tukey test, $p = 0.025$) and samples 3 and 6 (Tukey test, $p = 0.006$). The statistical difference between samples 1 and 3 reflects a morphological decrease in the size of the byssal notch and distance of the maximum height from the hinge and an increase in anterior auricle size, while the difference between samples 3 and 6 indicates a morphological decrease in anterior auricle size and an increase in the distance between

the hinge and the maximum length. These are the only samples between which there is a significant difference (tables 2 and 3). These differences while not significant enough to distinguish *C. middlesexensis* and *C. jeffersonius* as separate species are likely important to the variation of the genus as a whole.

	2	3	4	5	6
1	0.907	0.028	0.333	0.398	0.664
2		0.320	0.843	0.943	0.998
3			0.999	0.897	0.501
4				0.998	0.947
5					0.994

Table 2: Tukey test results for principal component 1 values
P values for comparison between means of principal component 1 values for each sample. Highlighted values are those for which the comparison is significant.

	2	3	4	5	6
1	0.196	0.025	0.962	0.264	1.000
2		0.987	0.858	1.000	0.095
3			0.500	0.961	0.006
4				0.911	0.923
5					0.141

Table 3: Tukey test results for principal component 2 values
P values for comparison between means of principal component 2 values for each sample. Highlighted values are those for which the comparison is significant.

The differences between samples 1 and 3 and 3 and 6, as well as the lack of differences between all other samples, are best visualized when principal components 1 and 2 are represented graphically through time (figures 12 and 13). Despite the previously mentioned differences, the majority of the samples are not significantly different from each other, as illustrated by the large overlap in error bars. This further emphasizes the overall trend of equivalent within-species variation and between-species

variation, which suggests that *C. middlesexensis* and *C. jeffersonius* cannot be differentiated based on landmarks. Thus, field identification must rely on other characters.

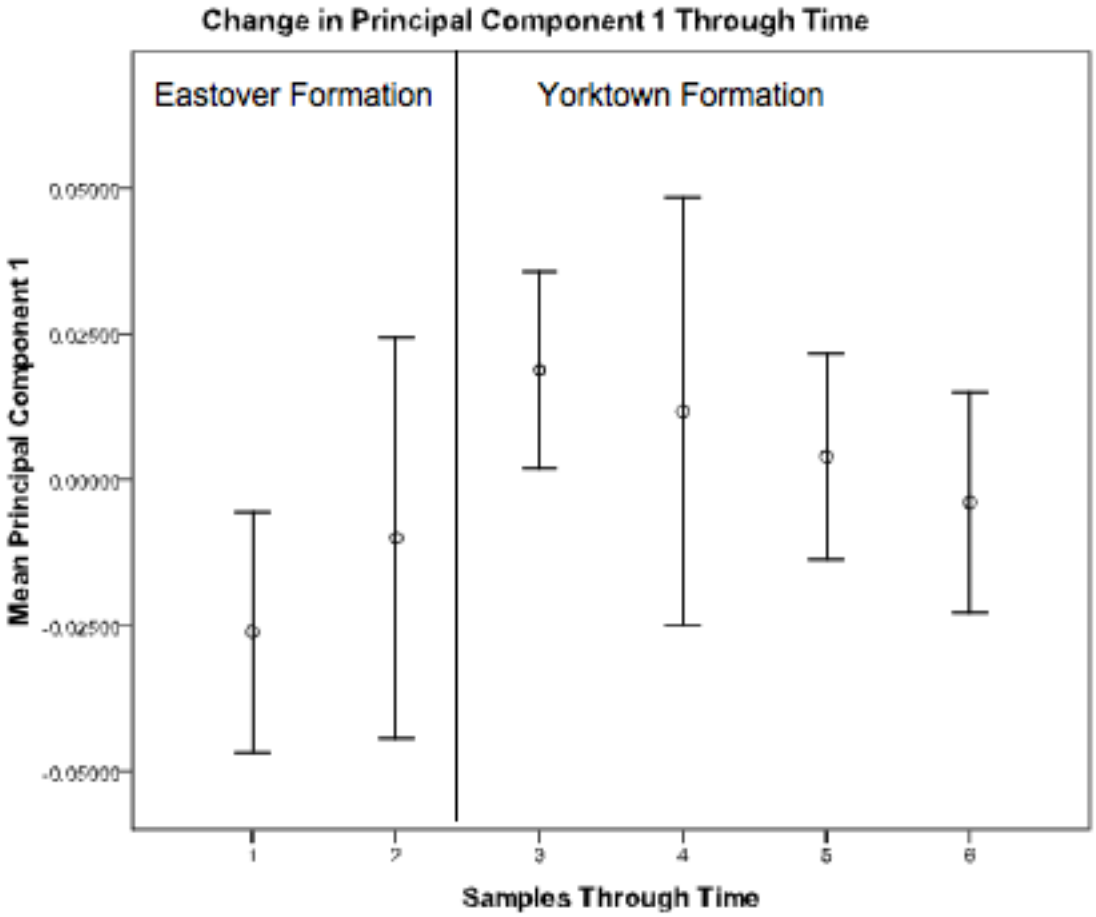

Figure 12: Change in principal component 1 through time
Means are graphed with 95% confidence interval error bars. The overlap of error bars of most samples indicates that variation between most samples is not significant. The only significant difference exists between samples 1 and 3 ($F_5 = 2.339$, $p = 0.05$; Tukey test, $p = 0.028$). A line representing the unconformable contact between the Eastover and Yorktown Formations divides the graph into samples that are commonly accepted as *C. middlesexensis* and samples that are commonly accepted as *C. jeffersonius.*

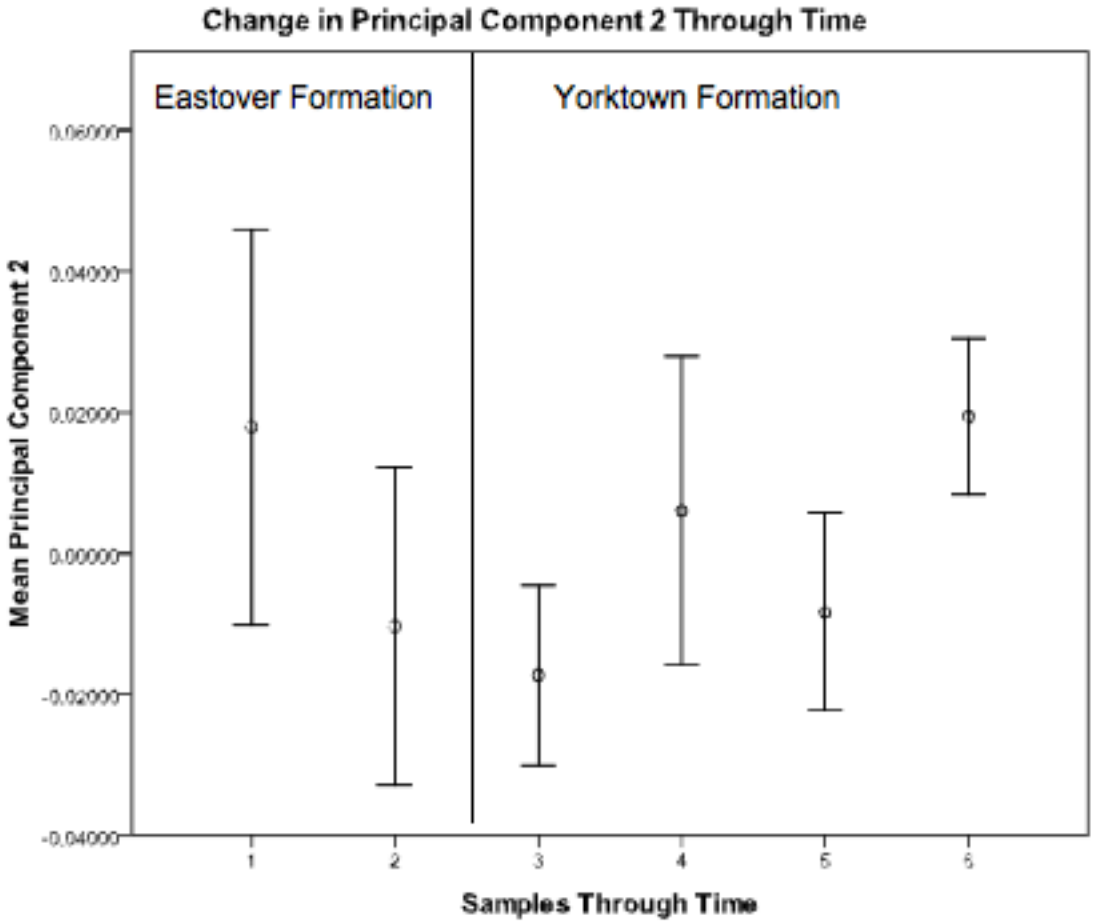

Figure 13: Principal components through time
Means are graphed with 95% confidence interval error bars. There is less overlap between samples than there is with principal component 1 values, but the only differences that are significant are between samples 1 and 3 ($F_5 = 4.096$, $p = 0.002$; Tukey test, $p = 0.025$) and samples 3 and 6 ($F_5 = 4.096$, $p = 0.002$; Tukey test, $p=0.006$). A line representing the unconformable contact between the Eastover and Yorktown Formations divides the graph into samples that are commonly accepted as *C. middlesexensis* and samples that are commonly accepted as *C. jeffersonius*.

The significant difference between samples 1 and 3 likely indicates a difference between *C. middlesexensis* and *C. jeffersonius*, but sample 2 is not significantly different from either sample 1 and 3, even though its stratigraphic distribution indicates that it should be a different species from sample 3. This suggests that the two species, as they

currently are defined are not different from each other based on these landmarks. If they were different, then samples 2 and 3, between which lies the boundary between the Eastover and Yorktown Formations, would have statistically significant differences in principal component values. Or if the evolution of the species were truly gradualistic, then, if samples 2 and 3 were not different, differences between sample 2 and other species would increase with sample size such that 2 and 4 are more different that 2 and 3, and so on. However, these results do not indicate any significant difference between sample 2 and any other sample. Instead, data suggests that evolution of *Chesapecten* through time appears not consistent with the gradualistic mechanism that is based stratigraphy and that species might not be well defined.

It is additionally important to note that *C. jeffersonius* represents a peak and trough in principal component values. For principal component 1, for example, values increase for samples 1-3 and then decrease for samples 4-6. The opposite occurs, but not as strongly in principal component 2, which decreases during the first half of the samples and increases overall in the second half. This suggests that these may be morphological features of *C. jeffersonius* that differentiates it from *C. middlesexensis* and *C. madisonius*. Also it is likely that gradual change is occurring in principal component 1, which is based primarily on variation of the byssal notch. This means that the size of the byssal notch is gradually decreasing over time.

Morphology through time

Discrete and continuous character data were used to assess changes in morphology of eight species of *Chesapecten* through time in order to identify any genus-wide trends. These data are depicted in figures 14-18. Characters represented are those

that are typically used to distinguish species. For each species, the means and standard errors of the character values were graphed against stratigraphic time in order to identify genus-wide trends in morphology. Results of most characters indicate little to no general trend across the majority of species, with only an individual species differing from the rest of the genus.

Byssal notch size is quantified as a ratio relative to the total anterior auricle length. This provides a measure of the extent to which the byssal notch extends into the anterior auricle and standardizes this measurement relative to size of the individual. *C. coccymelus* and C. *nefrens* have the largest byssal notch out of all species and *C. jeffersonius* has the smallest byssal notch. There is a significant overall decrease in byssal notch size over time ($KW_7 = 34.733$, $p<0.001$). This suggests that size of the byssal notch maybe an important feature in species identification and understanding genus-wide evolution, and is corroborated with field specimen results, which highlight the importance of the byssal notch in contributing to variation between species. Miyazaki (1978) also observed this decrease in byssal notch.

The byssal notch, which facilitates the attachment of byssal fibers to sediment, has been correlated with life history (Stanley 1972). Stanley (1972) identified two different life histories for scallops: life-long byssal attachment and attached juveniles that develop free-swimming abilities as adults. The evolution of free-swimming behavior in Pectinidae directly correlates with the decrease in byssal notch, a feature that is important for stabilization when attached, but which hinders swimming ability in unattached individuals. This family-wide evolutionary pattern is evident at the genus level in *Chesapecten*, although free-swimming traits developed at the family level during the

Paleozoic. The high abundance of the younger species of *Chesapecten* coincides with an increase in abundance of *Argopecten*, which displays a similar life habit, in California (Smith and Jackson 2009). Perhaps there were environmental conditions selecting for an attached and free-swimming life history. It is important to note that *Argopecten* diversity significantly declined during the late Pliocene, which is the same time that *Chesapecten* went extinct (Smith and Jackson 2009).

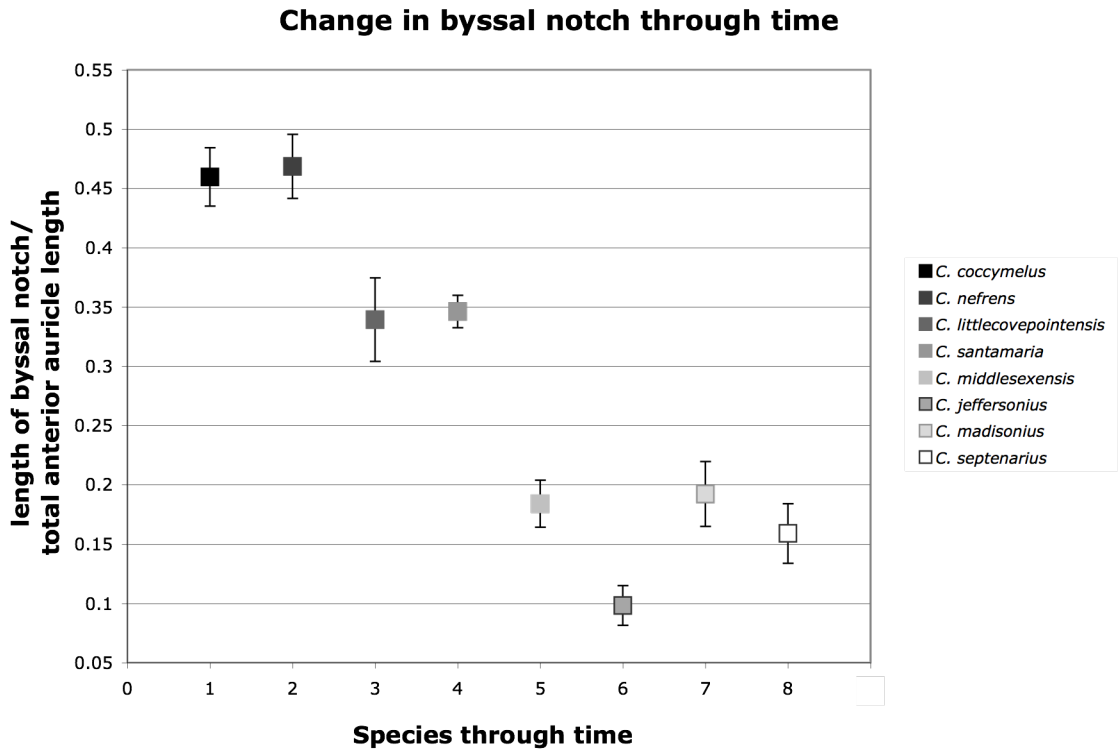

Figure 14: Size of byssal notch through time
Points were generated for the mean and standard error of the values for each species. Byssal notch length was divided by anterior auricle length to standardize for the size of individuals. Average size of the byssal notch significantly decreases in the genus over time ($KW_7 = 34.733$, $p<0.001$).

Shape was quantified using a ratio of the maximum height to maximum length, which determined whether individuals were longer than they were tall and vice versa, while also standardizing for size. Adult *Chesapecten* have been defined as having a

greater length than height (Ward and Blackwelder 1975). Results indicate that this is true for all species except *C. coccymelus*, which is the only species with a mean ratio greater than 1. This ratio is significantly greater than that of all other species, while the ratio of *C. nefrens* is significantly less than that of all other species. The younger species have relatively consistent ratios, with a slight decrease at *C. middlesexensis* and *C. jeffersonius*. This character is consistent with the genus description in the literature, but *C. coccymelus* is an obvious outlier. There is a significant difference between *C. coccymelus* and the other species ($KW_7 = 21.684$, $p = 0.003$), which is fairly obvious from visual observation of the specimens.

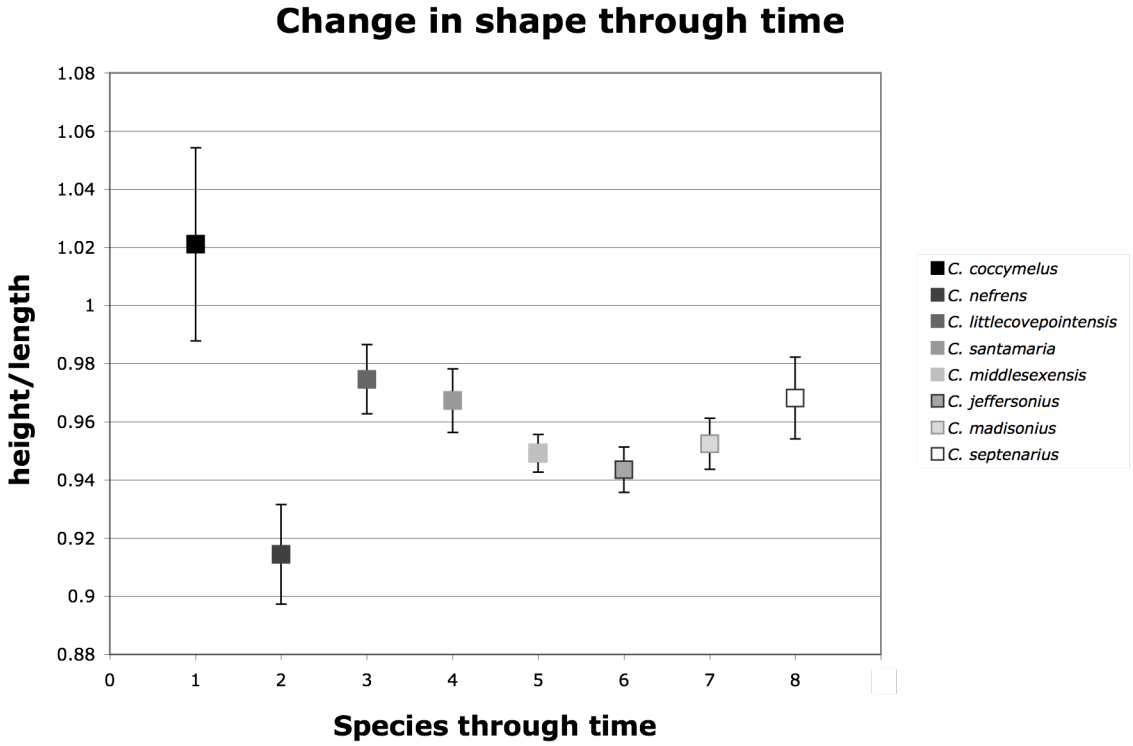

Figure 15: Shell shape through time
Points were generated for the mean and standard error of the values for each species. A ratio less than 1 indicates that individuals are longer than they are tall. Ratios are relatively consistent across the genus, with a few exceptions, but there are some significant differences ($KW_7 = 21.684$, $p = 0.003$).

In order to standardize size for a cross-genus comparison, the geometric mean was calculated from the measured height and length of each individual. Variability in this trait is quite large with standard error for most species at about ± 5 millimeters (figure 16). *C. coccymelus* is much smaller than all other species, and *C. nefrens* and *C. jeffersonius* are slightly larger. This further highlights the significance of the difference between *C. coccymelus* and the rest of the genus ($KW_7 = 36.084$, $p<0.001$), as specimens used in this analysis were some of the largest known from this species (Ward, pers. comm. 2010). The largest species is *C. jeffersonius*, which occurs as a peak at the end of a period of increasing size. Species younger than *C. jeffersonius* are much smaller. A possible explanation for the peak in size at *C. jeffersonius* is increased nutrient availability. The amount of available nutrients is very important to modern scallops, as growth rates can range from 0.3 mm/week when water temperatures are warmer to 1.5 mm/week during periods of cold upwelling (Shumway and Parsons 2006). It is likely that changes in the size of *Chesapecten* are related to changes in environmental conditions such as nutrient supply. There is evidence of increased cold-water upwelling during the early Pliocene (Stanley 1986). Increased upwelling would have increased the nutrient supply and could have resulted in an increase in *Chesapecten* size.

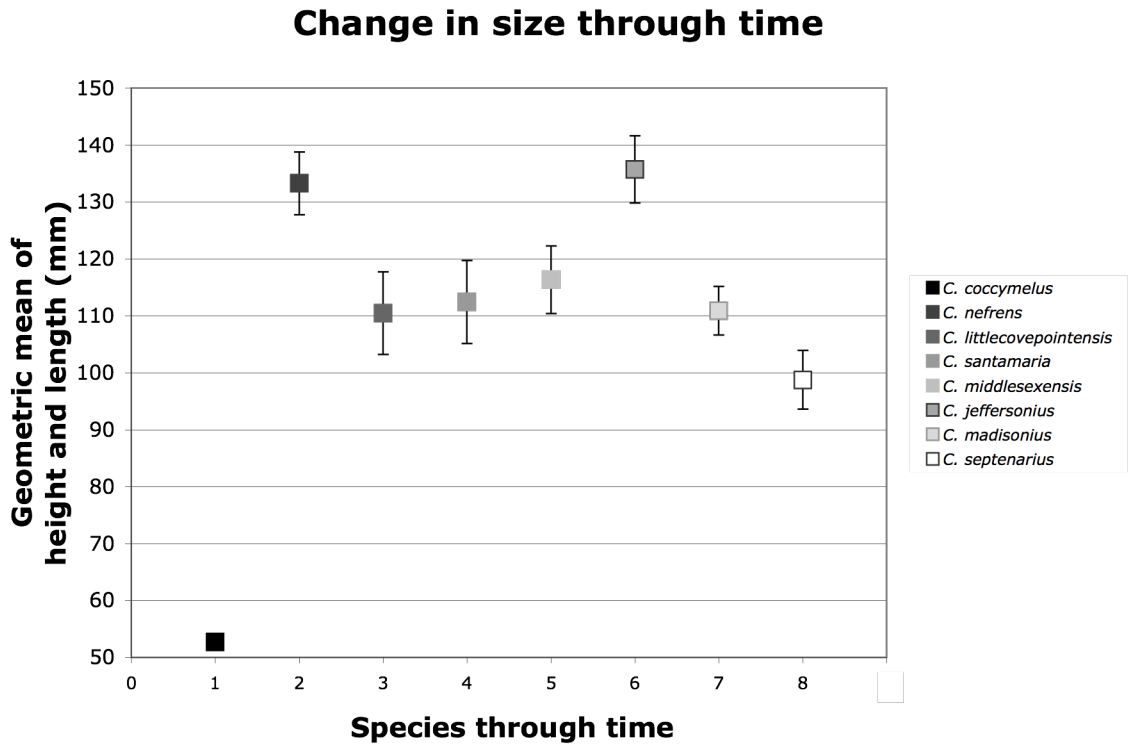

Figure 16: Shell size through time
Points were generated for the mean and standard error of the values for each species. *C. coccymelus* is much smaller than all other species, while *C. nefrens* and *C. jeffersonius* are much larger. There is a general increase in size over time until a peak at *C. jeffersonius*, after which size decreases ($KW_7 = 36.084$, $p<0.001$).

Rib count is very consistent within species, as evident by the reduced error bars (figure 17), but there are significant differences between some species ($KW_7 = 63.379$, $p<0.001$). This trait is very similar (at about 14-15 ribs) for all species except *C. jeffersonius* and *C. septenarius*, which have significantly fewer ribs (about 8), and *C. coccymelus*, which has significantly more ribs (about 16). *C. santamaria* has slightly fewer ribs than some other species (about 13-14), but this difference is not consistently significant. The similarity between rib count for most species suggests that, with the exception of distinguishing *C. jeffersonius* and *C. septenarius* from the rest of the genus, it is probably not a good character to use in order to differentiate species. For example,

rib count can be used to distinguish between *C. middlesexensis* and *C. jeffersonius* but it cannot distinguish between *C. middlesexensis* and *C. madisonius.* Based on the highly significant difference of the rib counts of *C. jeffersonius* and *C. septenarius* in this study and the fact that both have almost the same average rib count suggests that these two species might be closely related since rib size has a strong genetic basis (Wilbur and Gaffney 1997).

The measured values presented in this study differ from those reported by Ward and Blackwelder (1975), which suggest more variation within species based on a similar sample size. This additional variation further complicates the use of rib count as a species identifier for the genus, as it creates the possibility that rib counts of *C. jeffersonius* overlap with other species, particularly *C. middlesexensis* and thus cannot be used as a consistent identifying trait.

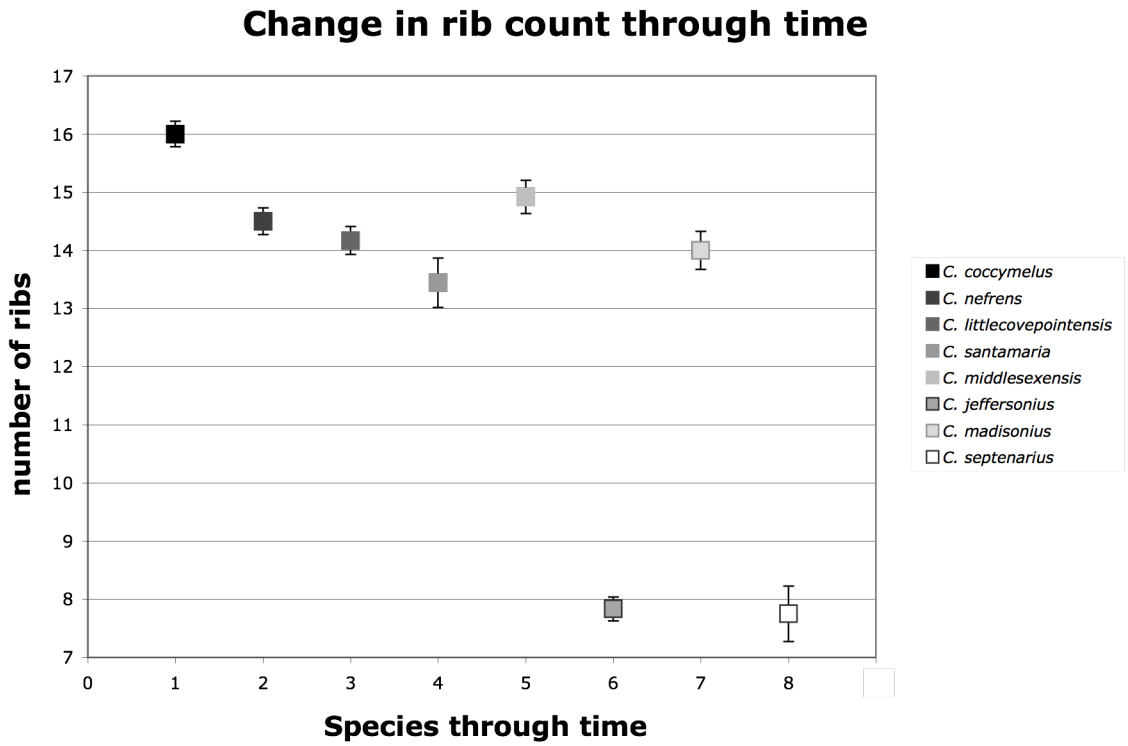

Figure 17: Rib count through time
Points were generated for the mean and standard error of the values for each species. The rib counts of *C. jeffersonius* and *C. septenarius* are significantly less than that for all other species ($KW_7 = 63.379$, $p<0.001$).

Rib cross-sectional shape is a highly variable trait, as indicated by the large error bars, although it is possible that much of this variation is due to inherent variability in the method of identifying discrete variables. The majority of the species have ribs that are more rounded than they are square, with *C. coccymelus*, *C. middlesexensis* and *C. septenarius* as notable exceptions. Based on these data, both *C. coccymelus* and *C. septenarius* can be classified as having mostly square ribs, while *C. middlesexensis* should be considered to have intermediate shaped ribs. Among the species with round ribs, there is a slight increase in roundedness over time. The ribs of *C. septenarius* are significantly squarer than most other species ($KW_7 = 28.036$, $p<0.001$).

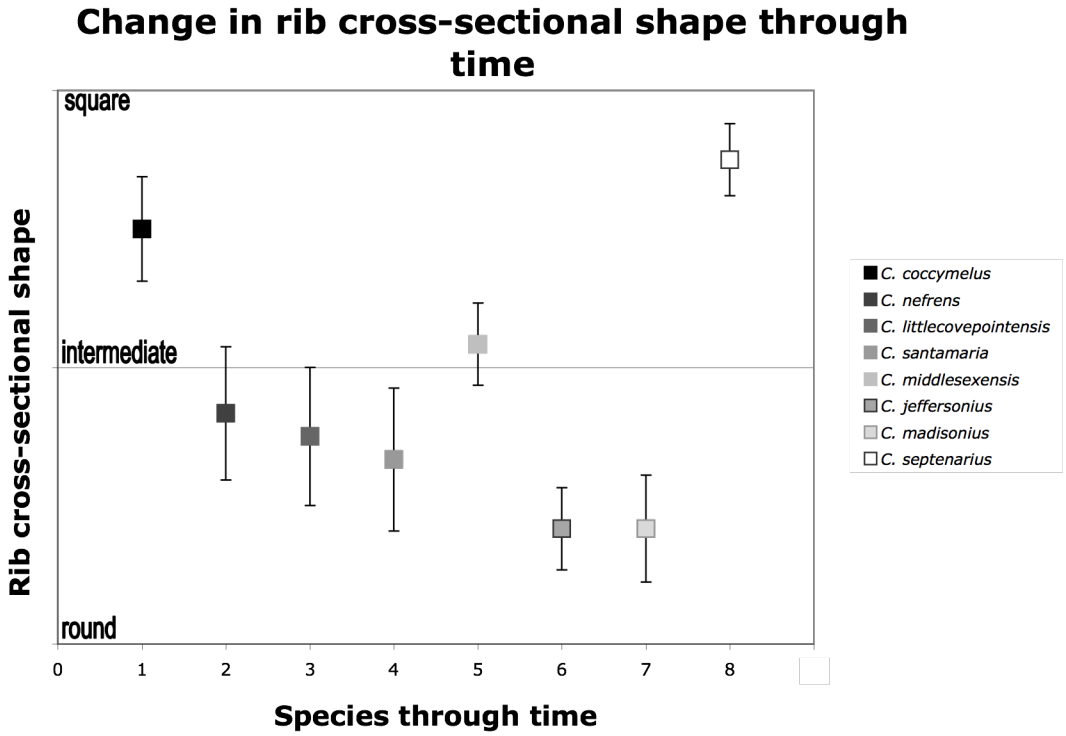

Figure 18: Rib cross-sectional shape through time
Points were generated from the mean and standard error of the values for each species. Most species have rounded ribs, although high variability in the trait makes definite results difficult to determine. However, it is clear that the ribs of *C. septenarius* are much more square than those of all other species ($KW_7 = 28.036$, $p<0.001$).

Phylogenetic relationships

A phylogeny was created to examine the evolutionary relationships among species of *Chesapecten*. In creating a phylogeny, *C. coccymelus* was designated as the outgroup. With this designation, a parsimony-based analysis of the 39 unordered discrete and continuous measured characters produced a single most parsimonious tree (figure 19) with a length of 8.617. The tree was fully resolved with a total fit of 37.19 and adjusted homoplasy of 0.81. Based on this evolutionary sequence, *C. jeffersonius* and *C. septenarius* are the most closely related species. These results are different from what

would be expected given the accepted stratigraphic sequence and assumed anagenetic relationship in which each species becomes extinct after evolving into its descendent.

Tree length is based on the length of each of the branches, which is a factor of the number of state changes that occur along the branch. Branch lengths are depicted in figure 20, with longer branches indicating more state changes along the branch. *C. nefrens* and *C. jeffersonius* have the longest branches at 0.721 an 0.811, which suggests that they have a high number of autapomorphies and thus have a lot of characters that make them unique from other species. As the most unique species, *C. nefrens* and *C. jeffersonius* have a lot of characters that can distinguish them from the rest of the genus. In contrast, there is a very short branch length (0.000) at the node between *C. santamaria* and *C. coccymelus*, which means that there are not many characters that differentiate the two. This lack of synapomorphies suggests that *C. santamaria* exhibits an ancestral morphology despite being located stratigraphically in the middle of the sequence. A list of synapomorphies that support each node and the autapomorphies that support each species is included in Appendix D.

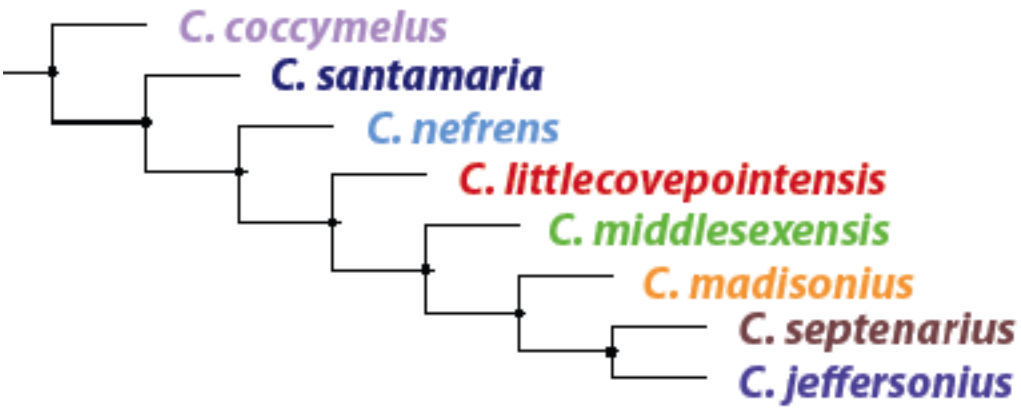

Figure 19: Phylogeny
C. coccymelus was designated as the outgroup, generating a single most parsimonious tree. The evolutionary relationships present in the tree differ from those suggested by the accepted stratigraphy. *C. jeffersonius* and *C. septenarius* are the most closely related species.

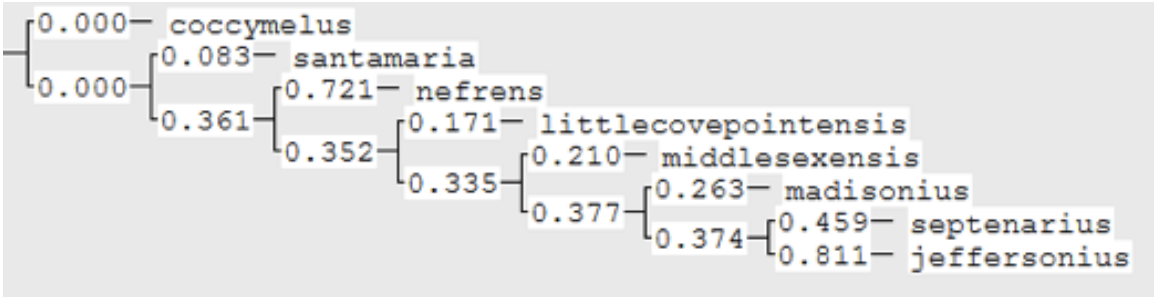

Figure 20: Branch lengths
Numbers indicate the length of each branch. *C. jeffersonius* and *C. nefrens* have the longest branches and are thus more distinct from other species.

Random sampling of the tree using bootstrapping indicates that all but two nodes are well supported (figure 21A). The two nodes that are not well supported are the ones between *C. littlecovepointensis* and *C. nefrens* and between *C. jeffersonius* and *C. septenarius*. These nodes can be collapsed to create polychotomies, which are nodes from which there are more than two branches (figure 21B).

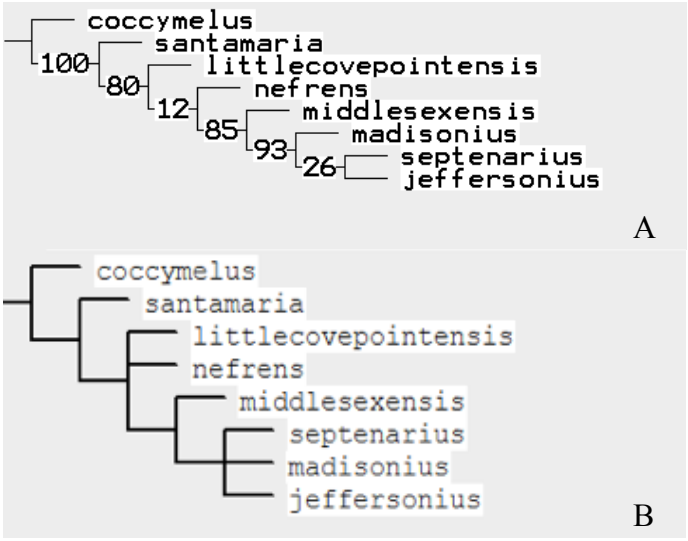

Figure 21: Bootstrapping values
(A)Values indicate the support for each node, with well-supported nodes having values greater than 70. (B) Tree with unsupported nodes collapsed.

Based on this assessment it appears that *C. middlesexensis* evolves into *C. septenarius*, *C. madisonius*, and *C. jeffersonius*. This evolutionary sequence of *Chesapecten* differs from the stratigraphic sequence (figure 22), which places *C. jeffersonius* as a direct descendent of *C. middlesexensis* and an ancestor to both *C. madisonius* and *C. septenarius*. *C. santamaria* is also out of stratigraphic order in this phylogeny; it occurs between *C. coccymelus* and *C. nefrens* instead of *C. nefrens* and *C. littlecovepointensis*. These differences are highlighted by the comparison of branching

order in the phylogeny to the branching order that would be expected if the phylogeny followed the stratigraphic sequence (figure 21).

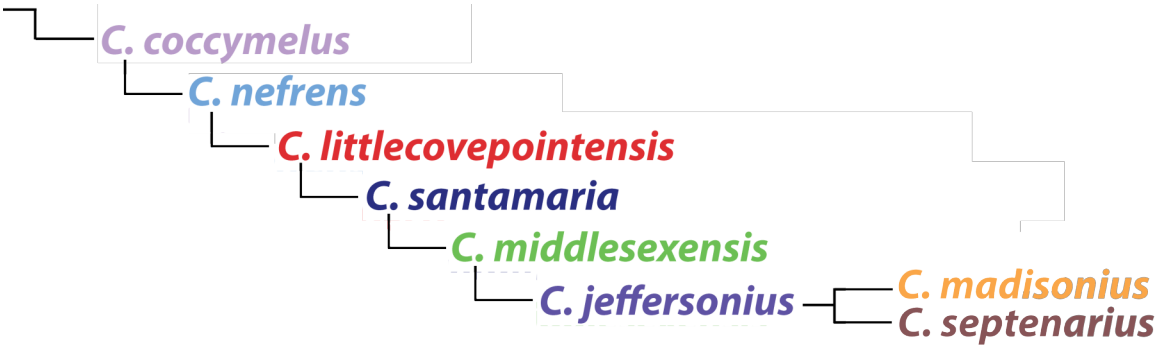

Figure 21: Expected phylogeny based on stratigraphy
Species arranged in the expected phylogenetic sequence given the known stratigraphic sequence and accepted anagenetic pattern of evolution of *Chesapecten.* This sequence is different from the phylogeny produced by a parsimonious analysis of discrete and continuous characters.

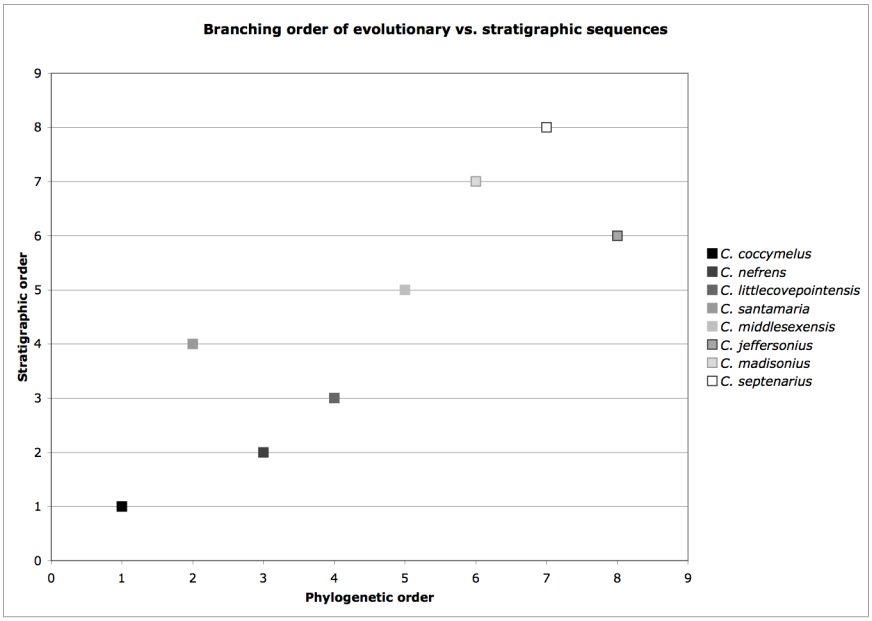

Figure 22: Branching orders in evolutionary vs. stratigraphic sequences
If the branching orders for both sequences were the same, this plot would be linear with a constant slope of 1. Since it is not linear and the slope changes, there are major differences between the two sequences.

Differences between the phylogeny and stratigraphic sequence could be the result of ecophenotypic variation in the genus, which suggests that the evolution of *Chesapecten* could be more complicated than the widely accepted anagenetic sequence in which each species gradually evolves into the next over time. There are several morphological traits, such as size and byssal notch, that change in a manner that can be explained by changes in environmental conditions. This could result in convergence of characters, in which the same trait evolved independently in two different species. It is also possible that there are gaps in the stratigraphic record and species ranges actually cross, as opposed to ending at, stratigraphic contacts. For example, the only species found in the Sunken Meadow Member of the Yorktown Formation is *C. jeffersonius*. This creates a missing evolutionary link because if, as suggested by the evolutionary sequence, *C. madisonius*, *C. septenarius*, and *C. jeffersonius* are derived from a common ancestor, the stratigraphic range of that ancestor should be connected to the stratigraphic ranges of all three of its descendents, which suggests that there should be some intermediate species occurring in the Sunken Meadow Member along with *C. jeffersonius*.

Discussion

As indicated by the results, the morphology and phylogeny of *Chesapecten* is quite complicated, but a better understanding of the evolutionary and morphological patterns of the genus can be derived from combining the three components of this study, as the results from each can inform the others.

The results of research question one, which identified morphological shape as an insufficient trait for the differentiation of *C. middlesexensis* and *C. jeffersonius*, can be

corroborated with the results of question two, the analysis of morphological change through time, which shows no significant difference between these two species based on shape. However, all of the other morphological characters analyzed do show significant differences between the two species, which suggests that perhaps features such as byssal notch length, overall size and rib count are suitable traits to differentiate *C. middlesexensis* from *C. jeffersonius*. Additionally, the results of question three, the phylogeny, which defines species based on the phylogenetic species concept, confidently defines *C. middlesexensis* and *C. jeffersonius* as separate species. Given the significant differences highlighted by two different species concepts, it is reasonable to conclude that *C. middlesexensis* and *C. jeffersonius* are distinctly different species.

This conclusion, however, does not reconcile the difficulty in identifying field specimens of the two species that occurs even when using characters that show clear differences between museum specimens. An explanation for the high variability within samples of the field specimens could be that some samples actually contain more than one species or hybrids of the two species. This would suggest that the stratigraphic ranges of species do not fall neatly within the boundaries of sedimentary units. For example, it is possible samples from the Sunken Meadow Member contained an intermediate between *C. middlesexensis* and *C. septenarius* and *C. madisonius*. In fact, this should be expected if the phylogenetic results linking these three species to a common ancestor are correct. If this is the case, and there are intermediates in the Sunken Meadow Member, this could both explain the high variability within field samples as well as solve part of the evolutionary and stratigraphic sequence discrepancy that was created from the phylogenetic results.

The answers to research questions two and three, which assess morphology though time and phylogenetic relationships, are inherently linked because they involve the same set of data. Traits that over time evolve in specific patterns can provide insight into the evolutionary mechanisms affecting the genus. For example, the fact that the length of the byssal notch decreases through time reflects an evolutionary adaptation to a free-swimming lifestyle, a behavior that is likely a response to predation since swimming is a method of escaping danger. Perhaps this trait represents the predator-prey relationship between scallops and their primary predators, sea stars and gastropods. If the predators in its environment evolved to counter previous defense mechanisms, *Chesapecten* could have responded by adopting a free-swimming lifestyle. An understanding of the reasons for the evolution of *Chesapecten* can be obtained from analyzing how morphology changes through time. This can inform the phylogenetic analysis especially in figuring out what is responsible for the difference between the expected stratigraphic sequence and the resulting evolutionary sequence.

Another interesting result from these analyses is the general uniqueness of *C. jeffersonius*. The high branch length and large number of autapomorphies, as determined by the phylogeny, indicate that there are a lot of character states that occur only in specimens of *C. jeffersonius*. This species is also often an outlier in the morphology through time results, that is, for many traits (byssal notch length, size, and rib number), *C. jeffersonius* exhibits a character state that is significantly different from the character states exhibited by most of the other species. With such distinct traits, it is possible that *C. jeffersonius* lived during an atypical environment, one with an abundant nutrient supply but also a large population of well-adapted predators (as evidenced by its

extremely large overall size and extremely small byssal notch). Other species have similar traits, for example *C. middlesexensis, C. madisonius,* and *C. septenarius* also have small byssal notches, suggesting some similarity between environmental conditions, but the average length for *C. jeffersonius* is still more extreme.

Although the analyses agree about many aspects of *Chesapecten* morphology and evolution, there are also points at which there is some disagreement. For example, the principal components analysis suggests possible gradual change over time in principal component 1. This conclusion can also to some extent be drawn from some of the character analyses of morphological change through time. However, the phylogeny does not indicate that species are evolving gradually, although it does not definitively suggest that they are not.

Overall the three components of this study create a unified understanding of *Chesapecten* such that almost all species can be considered distinct species, as defined by both the morphological and phylogenetic species concept. Additionally, changes in morphology throughout time as well as the evolutionary sequence are complicated. This complication is likely the results of ecophenotypic variation or gaps in the fossil record. However, through a holistic examination of *Chesapecten* morphology and phylogeny, it is possible to begin to piece together an explanation of how this genus is evolving, an answer that is intricately linked with understanding how differences in morphological characters change between species and how these changes serve to inform species definitions.

Future Work

Further work is needed to test the extent to which environmental conditions influenced the change in *Chesapecten* morphology over time as well as the extent to which gaps in the fossil or stratigraphic records affect the preservation of these changes. This should be examined at known time intervals and by analyzing samples of sediment and *Chesapecten* that are found in the same unit and at the same locality and comparing morphological signals for environmental change with sedimentological evidence of actual changes. This is necessary in order to confidently generate a phylogeny for the genus.

Additional future work should relate the evolutionary sequence of *Chesapecten* to individual ontogeny. The sequence likely paramorphic, but further observation is necessary to fully test this hypothesis. This would involve establishing growth rates by microsampling growth lines and using delta ^{18}O ratios to determine seasonality.

Finally, the discrete and continuous characters examined in this study, especially those such as byssal notch and rib number that may be important for field identification of *C. middlesexensis* and *C. jeffersonius*, should be measured on field specimens in order to quantify the differences between these two species. This will provide a better system for field identification and a better understanding of how these traits change over stratigraphic time.

Conclusions

This study involved both a quantitative assessment of the between-species relationships of morphological traits and the construction of a phylogeny to identify evolutionary relationships in the genus *Chesapecten*. The morphological analysis

demonstrated that there is at least as much variation within species and samples as there is between groups, which means that *C. middlesexensis* and *C. jeffersonius* cannot be distinguished based on landmarks describing morphological shape. However, with a character analysis, almost all species can be differentiated from the others based on a combination of traits. For example, *C. middlesexensis* can probably be distinguished from *C. jeffersonius* based on rib count, but this character does not provide as good of a distinction from *C. madisonius*. Results of the phylogeny indicate that evolutionary relationships might be different than the anagenetic sequence that is widely accepted based on stratigraphy. This raises the possibility that ecophenotypic variation plays a significant role in the evolution of *Chesapecten*, and additionally suggests that the fossil record might be incomplete.

There are, however, still uncertainties about the evolutionary sequence of *Chesapecten* and how this sequence is affected by ecological conditions, so further examination of the relationship between morphology and environment is needed to develop a complete understanding of the evolution of *Chesapecten*. However, results of this study are significant as it is one of the first quantitative analyses of many of the commonly accepted features of the genus. Because of this, these findings will add to the scientific knowledge base for the fields of paleontology and evolutionary biology. Furthermore, this study lays the foundation for understanding the effects of ecological conditions on shell morphology as well as the preservation potential of that morphology, which are both important to the general understanding of the paleoenvironment of the mid-Atlantic Miocene and Pliocene Coastal Plain.

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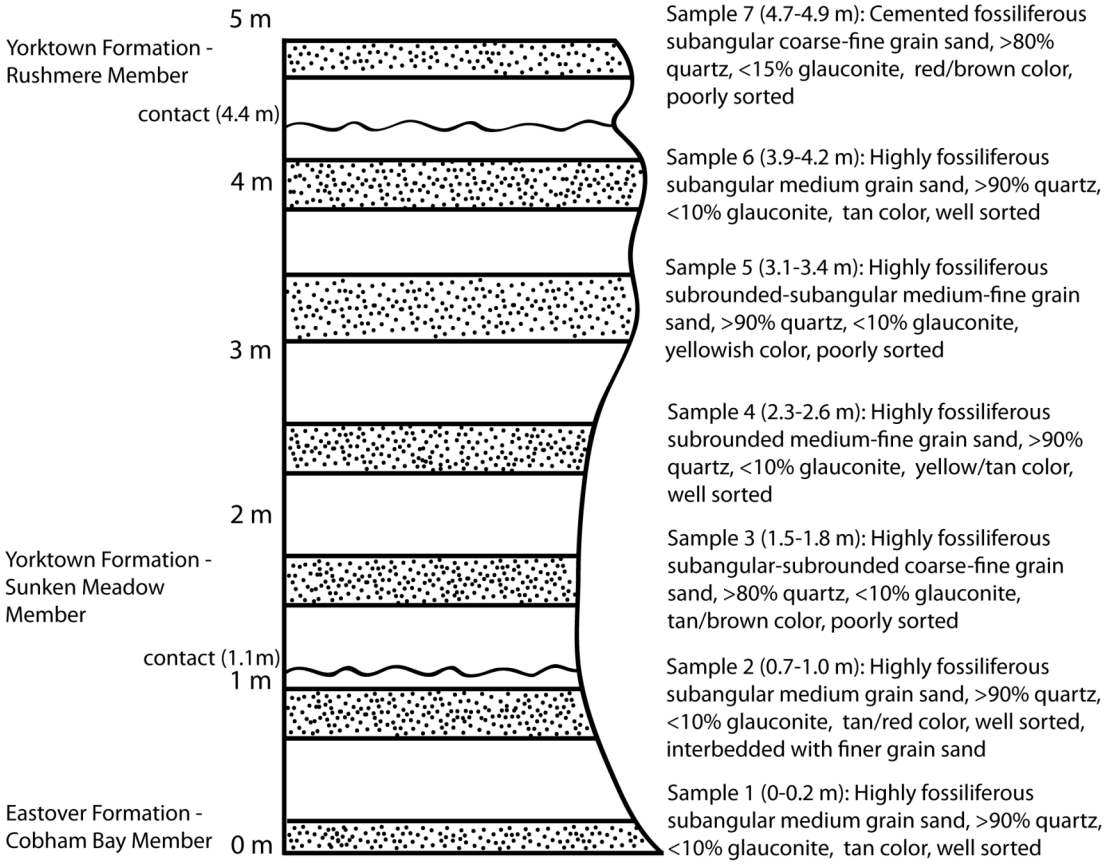
Appendices

Appendix A: Stratigraphic section of cliff sampled at Cobham Wharf



Appendix B: Morphological and phylogenetic characters

Measurements

1. Maximum height (mm) – from hinge to commisure, greatest distance perpendicular to hinge
2. Maximum length (mm) – greatest distance anterior to posterior that is parallel to hinge
3. Height/length – ratio to measure overall shape
4. Geometric mean – to measure overall size = $(h*l)^{1/2}$
5. Total number of ribs
6. Width of center rib at commisure (mm)
7. Width of center interspace at commisure (mm)
8. Height of center rib at commisure (mm) – measured from bottom of interspace to top of rib
9. Anterior auricle length (mm) – from umbo to anterior-most extent of outer ligament
10. Posterior auricle length (mm) – from umbo to posterior-most extent of outer ligament
11. Total auricle length (mm) – anterior-most extent to posterior-most extent of outer ligament
12. Anterior auricle length/total auricle length – ratio to standardize anterior auricle length for size
13. Posterior auricle length/total auricle length – ratio to standardize posterior auricle length for size
14. Total auricle length/total length – ratio to standardize total auricle length for size
15. Length of byssal notch (mm) – measured from extent of anterior auricle to point at which auricle meets the rest of the shell
16. Length of byssal notch/length of anterior auricle – ratio to standardize byssal notch length for size
17. Resilium height (mm) – measured from umbo to ventral-most point of resilium perpendicular to hinge line
18. Resilium length (mm) – measured at ventral most edge, from anterior to posterior extents
19. Resilium height/resilium length – ratio to standardize for size
20. Resilium height/total height – ratio to standardize for size

Discrete characters

21. Ratio of maximum height/length
    0 = longer than high (ratio <1)
    1 = equal length and height (ratio=1)
    2 = higher than long (ratio>1)

22. Auricle length comparison
    0 = posterior and anterior auricles equal
    1 = posterior auricle longer
    2 = anterior auricle longer

23. Ratio of resilium height/length
    0 = longer than high (ratio <1)
    1 = equal length and height (ratio=1)
    2 = higher than long (ratio>1)

24. Comparison of rib and interspace widths at commisure
    0 = widths are equal
    1 = interspaces are wider
    2 = ribs are wider

25. Degree of fanning
    0 = slight
    1 = intermediate
    2 = significant

26. Thickness of shell
    0 = thin
    1 = intermediate
    2 = thick

27. Overall convexity of shell
    0 = mostly flat
    1 = point of convexity lies primarily at umbo
    2 = point of convexity lies primarily at the center of the shell

28. Rib cross-sectional shape
    0 = rounded
    1 = intermediate
    2 = square

29. Interspace cross-sectional shape
    0 = rounded
    1 = intermediate
    2 = square

30. Prominence of ribbing across shell (how tall are the ribs)
    0 = ribs flat
    1 = intermediate
    2 = ribs significantly raised

31. Byssal fasciole
    0 = not broad
    1 = intermediate
    2 = broad

32. Cardinal crura
    0 = absent
    1 = reduced
    2 = present

33. Auricular denticles
    0 = absent
    1 = weakly present
    2 = present

34. Ctenolium
    0 = absent
    1 = reduced
    2 = present

35. Trace of outer ligament
    0 = narrow
    1 = intermediate
    2 = broad

36. Hinge teeth
    0 = absent
    1 = weakly present
    2 = present

37. Pallial line insertion
    0 = weakly expressed
    1 = moderately expressed
    2 = significantly expressed

38. Ornamentation appearance
    0 = smooth
    1 = intermediate
    2 = scaly

39. Scales
    0 = none/unidentifiable
    1 = fine scaled close together
    2 = coarse scales far apart

Appendix C: Character data

Asterisk indicates type locality for each species. The type locality for *C. jeffersonius* and *C. septenarius*, Yorktown, VA was not available for sampling. The type locality for *C. madisonius* is unknown.

species	location	Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
C. coccymelus	Plum Point, MD*		51.3	52.74	0.97	52.015	16	3.84	2.48	2.16	15.38	9.55	25.31	0.608	0.377	0.48	7.87	0.51	2.16	1.91	1.131	0.042
C. coccymelus	Plum Point, MD*		52.01	48.52	1.07	50.235	15	2.8	2.27	2.03	16.47	10.5	27.17	0.606	0.386	0.56	7.8	0.47	2.22	2.33	0.953	0.043
C. coccymelus	Plum Point, MD*		48.57	51.75	0.94	50.135	16	3.04	2.91	1.67	19.04	12.75	31.76	0.599	0.401	0.614	7.5	0.39	2.24	1.44	1.556	0.046
C. coccymelus	Plum Point, MD*		61.54	52.58	1.17	56.884	16	3.22	3.82	2.75	14.55	11.62	26.39	0.551	0.44	0.502	n/a	n/a	3.04	2.22	1.369	0.049
C. coccymelus	Plum Point, MD*		53.97	58.89	0.92	56.376	17	2.63	2.82	2.29	14.62	11.78	26.24	0.557	0.449	0.446	n/a	n/a	2.05	2.13	0.962	0.038
C. coccymelus	Plum Point, MD*		51.87	49.11	1.06	50.471	16	2.7	3.08	2.27	14.48	8.73	23.47	0.617	0.372	0.478	n/a	n/a	2.18	1.84	1.185	0.042
C. nefrens	Camp Conoy*		151.5	163	0.93	157.12	16	7.31	6.86	3.15	38.4	42.39	81.07	0.474	0.523	0.497	21.1	0.55	15	7.65	1.962	0.099
C. nefrens	Camp Conoy*		125.9	137.32	0.92	131.51	15	8.47	8.29	3.18	39.97	38.03	77.42	0.516	0.491	0.564	19.3	0.48	10.6	6.88	1.535	0.084
C. nefrens	Camp Conoy*		136.2	153.59	0.89	144.61	15	7.67	7.56	3.16	41.43	35.56	77.73	0.533	0.457	0.506	21.2	0.51	13.6	6.01	2.265	0.1
C. nefrens	Camp Conoy*		147.6	167	0.88	157.01	15	6.99	8.98	3.96	39.9	38.84	78.45	0.509	0.495	0.47	n/a	n/a	13.5	8.87	1.524	0.092
C. nefrens	Camp Conoy*		130.4	145.29	0.9	137.62	14	6.91	8.69	3.65	38.82	35.96	73.85	0.526	0.487	0.508	n/a	n/a	11.7	7.07	1.649	0.089
C. nefrens	Camp Conoy*		126.6	145.12	0.87	135.53	13	6.43	8.34	4.55	42.21	40.2	82.3	0.513	0.488	0.567	n/a	n/a	9.58	4.78	2.004	0.076
C. nefrens	Choptank River		141.1	154.3	0.91	147.53	14	7.71	8.96	4.35	39.77	39.14	78.7	0.505	0.497	0.51	15.8	0.4	14.1	7.24	1.945	0.1
C. nefrens	Choptank River		139.6	150.76	0.93	145.05	14	7.41	7.64	3.03	37.57	37.73	75.09	0.5	0.502	0.498	14.3	0.38	12	5.14	2.327	0.086
C. nefrens	Choptank River		114.8	127.86	0.9	121.16	14	8.01	7.98	3.16	37.27	30.6	68.26	0.546	0.448	0.534	18.3	0.49	9.33	6.06	1.54	0.081
C. nefrens	Choptank River		115.7	122.44	0.94	119	15	6	7.36	4.7	31.51	31.75	62.89	0.501	0.505	0.514	n/a	n/a	7.55	4.33	1.744	0.065
C. nefrens	Choptank River		93.85	104.71	0.9	99.131	14	5.23	5.26	2.28	30.69	28.26	59.2	0.518	0.477	0.565	n/a	n/a	7.12	4.74	1.502	0.076
C. nefrens	Choptank River		104.2	103.35	1.01	103.78	15	5.05	6.16	2.79	29.49	25.77	54.61	0.54	0.472	0.528	n/a	n/a	8.66	5	1.732	0.083
C. littlecovepointensis	Little Cove Point*		125.86	133.83	0.94	129.78	14	9.03	9.07	2.9	26.8	22.78	50.03	0.536	0.455	0.374	12.1	0.45	9.61	5.23	1.837	0.076
C. littlecovepointensis	Little Cove Point*		132.90	139.10	0.96	135.96	15	8.04	7.99	2.8	29.52	25.68	55.64	0.531	0.462	0.4	10.8	0.37	13.7	6.78	2.018	0.103
C. littlecovepointensis	Little Cove Point*		137.72	146.83	0.94	142.20	16	8.3	8.16	2.46	28.02	24.07	52.37	0.535	0.46	0.357	5.98	0.21	15.6	7.01	2.231	0.114
C. littlecovepointensis	Little Cove Point*		89.26	88.83	1	89.04	14	4.75	5.61	2.84	28.96	22.81	51.33	0.564	0.444	0.578	n/a	n/a	5.65	3.52	1.605	0.063
C. littlecovepointensis	Little Cove Point*		84.51	80.94	1.04	82.71	14	4.87	5.2	2.27	23.19	17.36	40.64	0.571	0.427	0.502	n/a	n/a	6.03	3.84	1.57	0.071
C. littlecovepointensis	Little Cove Point*		121.37	129.06	0.94	125.16	14	6.62	7.68	3.54	25.26	17.59	42.21	0.598	0.417	0.327	n/a	n/a	7.55	4.79	1.576	0.062
C. littlecovepointensis	Langley's Bluff		125.3	134.48	0.93	129.82	14	7.49	8.5	2.21	29.73	28.06	57.16	0.52	0.491	0.425	8.01	0.27	10.4	5.17	2.004	0.083
C. littlecovepointensis	Langley's Bluff		122.7	128.92	0.95	125.77	14	8	7.96	3.03	29.15	26.04	55.44	0.526	0.47	0.43	9.82	0.34	8.05	3.88	2.075	0.066
C. littlecovepointensis	Langley's Bluff		110	111.48	0.99	110.74	15	6.63	5.78	2.48	28.25	21.82	50.66	0.558	0.431	0.454	11.3	0.4	5.83	3.92	1.487	0.053
C. littlecovepointensis	Langley's Bluff		105.8	110.14	0.96	107.95	13	6.71	6.8	2.54	24.96	19.93	44.98	0.555	0.443	0.408	n/a	n/a	6.25	2.9	2.155	0.059
C. littlecovepointensis	Langley's Bluff		80.47	76.46	1.05	78.439	14	3.63	4.91	3.08	19.48	14.06	33.73	0.578	0.417	0.441	n/a	n/a	3.73	3.26	1.144	0.046
C. littlecovepointensis	Langley's Bluff		67.44	68.24	0.99	67.84	##	3.69	3.70	2.34	19.29	15.17	33.98	0.57	0.45	0.50	n/a	n/a	3.28	2.40	1.37	0.05
C. santamaria	Windmill Point*		109.8	108.96	1.01	109.37	15	5.97	5.81	2.36	27.43	20.28	47.49	0.578	0.427	0.436	9.15	0.33	5.29	4.61	1.148	0.048
C. santamaria	Windmill Point*		106.4	111.5	0.95	108.9	13	10.8	9.24	3.32	27.85	18.47	45.95	0.606	0.402	0.412	8.47	0.3	5.89	4.1	1.437	0.055
C. santamaria	Windmill Point*		122.6	129.61	0.95	126.08	15	8.47	8.45	3.72	30.57	26.02	56.66	0.54	0.459	0.437	11	0.36	7.17	5.63	1.274	0.058
C. santamaria	Windmill Point*		145.5	162	0.9	153.54	15	8.84	9.79	2.26	39.66	31.83	70.37	0.564	0.452	0.434	n/a	n/a	9.14	7.68	1.19	0.063
C. santamaria	Windmill Point*		122.1	121.29	1.01	121.71	13	9.23	9.56	2.62	28.5	21.08	48.52	0.587	0.434	0.4	n/a	n/a	7.62	5.39	1.414	0.062
C. santamaria	Windmill Point*		123.6	129.38	0.96	126.45	14	7.3	8.48	1.38	33.09	19.72	51.57	0.642	0.382	0.399	n/a	n/a	7.59	4.21	1.803	0.061
C. santamaria	Essex Mill		88.55	90.18	0.98	89.361	12	6.76	5.83	3.94	24.66	18.78	43.31	0.569	0.434	0.48	9.54	0.39	3.80	3.76	1.01	0.04
C. santamaria	Essex Mill		106.5	112.08	0.95	109.24	13	6.68	6.8	2.87	27.54	21.62	49.09	0.561	0.44	0.44	n/a	n/a	6.04	4.99	1.21	0.06
C. santamaria	Essex Mill		67.4	67.04	1.01	67.22	11	4.44	4.16	2.53	20.13	14.02	34.05	0.591	0.412	0.51	n/a	n/a	3.79	2.49	1.52	0.06
C. middlesexensis	Urbana Creek*		150.6	157	0.96	153.75	15	6.81	7.56	3.42	36.18	38	74.32	0.487	0.511	0.473	5.54	0.15	15	6.68	2.24	0.099
C. middlesexensis	Urbana Creek*		114.3	121.2	0.94	117.68	15	5.49	5.44	2.53	31.03	25.4	56.75	0.547	0.448	0.468	4.91	0.16	9.45	4.9	1.929	0.083
C. middlesexensis	Urbana Creek*		115.6	123.03	0.94	119.26	15	4.72	5.19	3.09	32.66	26.82	59.52	0.549	0.451	0.484	6.65	0.2	8.21	4.83	1.7	0.071
C. middlesexensis	Urbana Creek*		123.9	125.03	0.99	124.46	17	4.79	4.25	3.26	29.67	25.56	54.28	0.547	0.471	0.434	n/a	n/a	9.07	6.18	1.468	0.073
C. middlesexensis	Urbana Creek*		105	112.35	0.93	108.63	15	5.11	5.05	2.76	31.34	25.99	56.56	0.554	0.46	0.503	n/a	n/a	6.94	4.27	1.625	0.066
C. middlesexensis	Urbana Creek*		112.4	113.23	0.99	112.81	16	4.15	5.25	2.15	28.33	24.21	52.11	0.544	0.465	0.46	n/a	n/a	8.6	4.04	2.129	0.077
C. middlesexensis	Claremont		152.3	164.5	0.93	158.26	15	9.15	9.08	3.13	38.42	37.3	75.04	0.512	0.497	0.456	4.71	0.12	9.87	4.78	2.065	0.065
C. middlesexensis	Claremont		92.16	100.14	0.92	96.067	14	5.8	5.93	2.56	26.56	23.54	49.95	0.532	0.471	0.499	6.85	0.26	6.96	3.53	1.972	0.076
C. middlesexensis	Claremont		98.09	103.53	0.95	100.77	14	5.25	5.66	4.78	26.28	25.51	51.83	0.507	0.492	0.501	5.48	0.21	5.78	3.67	1.575	0.059
C. middlesexensis	Claremont		102.5	109.1	0.94	105.75	15	5.22	7.88	5.02	28.61	22.35	50.22	0.57	0.445	0.46	n/a	n/a	8.9	4.32	2.06	0.087
C. middlesexensis	Claremont		100.2	105.42	0.95	102.77	15	6.51	6.49	4.72	28.64	24.31	52.74	0.543	0.461	0.5	n/a	n/a	6.57	3.82	1.72	0.066
C. middlesexensis	Claremont		93.2	98.41	0.95	95.77	13	5.57	5.75	4.1	26.35	23.32	49.37	0.534	0.472	0.502	n/a	n/a	6.45	3.3	1.955	0.069

	Character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
species	location																			
C. coccymelus	Plum Point, MD*	0	2	2	2	0	0	1	1	2	2	2	2	1	2	0	2	0	2	2
C. coccymelus	Plum Point, MD*	2	2	0	2	0	0	1	2	2	2	2	2	1	2	0	2	0	1	2
C. coccymelus	Plum Point, MD*	0	2	2	2	0	0	1	2	2	2	2	2	2	2	0	2	0	2	2
C. coccymelus	Plum Point, MD*	2	2	2	1	0	0	1	1	2	2	n/a	2	1	n/a	0	2	0	2	2
C. coccymelus	Plum Point, MD*	0	2	0	1	0	0	1	2	2	2	n/a	2	1	n/a	0	2	0	2	2
C. coccymelus	Plum Point, MD*	2	2	2	1	0	0	1	1	2	2	n/a	2	1	n/a	0	2	0	1	2
C. nefrens	Camp Conoy*	0	1	2	2	1	1	0	0	2	1	1	1	1	1	2	1	0	2	2
C. nefrens	Camp Conoy*	0	2	2	0	2	0	0	2	2	0	2	1	2	2	0	1	0	2	2
C. nefrens	Camp Conoy*	0	2	2	0	2	2	0	0	2	0	2	1	1	2	1	1	1	2	2
C. nefrens	Camp Conoy*	0	2	2	1	1	2	2	1	1	2	n/a	1	1	n/a	1	1	1	2	2
C. nefrens	Camp Conoy*	0	2	2	2	2	1	2	2	2	1	n/a	0	1	n/a	0	0	1	2	2
C. nefrens	Camp Conoy*	0	2	2	1	1	1	2	0	2	1	n/a	1	1	n/a	0	0	1	2	2
C. nefrens	Choptank River	0	0	2	1	1	1	0	0	0	0	2	1	1	1	2	2	2	1	2
C. nefrens	Choptank River	0	0	2	0	2	1	0	0	0	0	2	1	2	1	1	1	0	2	2
C. nefrens	Choptank River	0	2	2	0	2	1	0	1	2	1	2	1	2	2	0	2	1	1	2
C. nefrens	Choptank River	0	0	2	1	2	1	2	2	2	2	n/a	0	1	n/a	0	0	0	1	2
C. nefrens	Choptank River	0	2	2	0	2	0	2	1	1	2	n/a	0	2	n/a	0	1	1	2	2
C. nefrens	Choptank River	1	2	2	1	2	0	2	1	1	1	n/a	0	1	n/a	0	2	1	2	2
C. littlecovepointensis	Little Cove Point*	0	2	2	0	0	0	0	1	2	1	2	1	0	1	1	1	0	1	2
C. littlecovepointensis	Little Cove Point*	0	2	2	0	0	2	0	1	2	1	2	1	0	1	2	1	0	1	2
C. littlecovepointensis	Little Cove Point*	0	2	2	0	1	2	0	0	1	1	2	1	0	1	2	1	0	1	2
C. littlecovepointensis	Little Cove Point*	1	2	2	1	1	1	1	2	2	2	n/a	0	0	n/a	0	1	0	1	2
C. littlecovepointensis	Little Cove Point*	1	2	2	1	0	2	1	0	2	2	n/a	0	0	n/a	0	1	0	1	2
C. littlecovepointensis	Little Cove Point*	0	2	2	1	0	1	1	0	2	2	n/a	0	0	n/a	0	1	0	1	2
C. littlecovepointensis	Langley's Bluff	0	2	2	1	2	0	0	1	1	1	2	1	0	1	2	2	0	1	1
C. littlecovepointensis	Langley's Bluff	0	2	2	0	1	0	0	0	2	2	2	1	0	2	0	1	0	1	1
C. littlecovepointensis	Langley's Bluff	0	2	2	2	1	0	0	0	2	2	2	1	0	2	0	1	0	2	1
C. littlecovepointensis	Langley's Bluff	0	2	2	0	1	0	1	2	2	1	n/a	1	0	n/a	0	0	1	1	2
C. littlecovepointensis	Langley's Bluff	1	2	2	1	0	0	1	0	2	2	n/a	1	0	n/a	0	0	0	1	1
C. littlecovepointensis	Langley's Bluff	0	2	2	0	0	0	1	2	2	2	n/a	1	0	n/a	0	0	1	1	1
C. santamaria	Windmilll Point*	1	2	2	0	1	0	0	0	2	2	2	1	0	1	0	1	0	1	1
C. santamaria	Windmilll Point*	0	2	2	2	1	0	0	0	2	2	2	1	1	2	0	0	0	1	2
C. santamaria	Windmilll Point*	0	2	2	0	1	0	0	1	2	1	2	1	2	1	0	1	0	1	2
C. santamaria	Windmilll Point*	0	2	2	1	2	1	1	0	2	1	n/a	1	1	n/a	0	1	0	2	2
C. santamaria	Windmilll Point*	1	2	2	1	1	1	1	0	1	1	n/a	0	1	n/a	1	1	0	1	2
C. santamaria	Windmilll Point*	0	2	2	1	1	0	1	1	1	1	n/a	0	1	n/a	1	1	0	0	2
C. santamaria	Essex Mill	0	2	2	2	1	0	0	2	2	2	2	2	2	2	0	1	1	2	2
C. santamaria	Essex Mill	0	2	2	1	2	0	1	0	2	2	n/a	1	0	n/a	0	1	0	1	2
C. santamaria	Essex Mill	1	2	2	2	0	0	1	2	2	2	n/a	2	2	n/a	0	1	1	2	2
C. middlesexensis	Urbana Creek*	0	1	2	1	0	1	0	1	1	1	1	1	0	0	2	2	0	1	2
C. middlesexensis	Urbana Creek*	0	2	2	0	0	1	0	1	1	1	1	1	0	1	2	2	0	2	2
C. middlesexensis	Urbana Creek*	0	2	2	1	0	1	0	1	1	1	1	1	1	1	0	1	1	2	2
C. middlesexensis	Urbana Creek*	0	2	2	2	0	1	1	1	1	2	n/a	0	0	n/a	1	1	1	2	2
C. middlesexensis	Urbana Creek*	0	2	2	0	0	1	1	2	2	2	n/a	0	0	n/a	0	1	0	2	2
C. middlesexensis	Urbana Creek*	0	2	2	1	0	1	1	0	0	1	n/a	1	1	n/a	0	1	0	1	2
C. middlesexensis	Claremont	0	2	2	0	1	1	2	1	0	2	2	1	0	0	1	2	0	0	0
C. middlesexensis	Claremont	0	2	2	1	1	1	1	1	1	1	2	1	0	0	0	1	2	0	1
C. middlesexensis	Claremont	0	2	2	1	1	1	1	1	1	2	2	1	0	0	0	1	2	0	1
C. middlesexensis	Claremont	0	2	2	1	1	1	1	2	2	2	n/a	1	0	n/a	2	2	1	0	0
C. middlesexensis	Claremont	0	2	2	0	1	1	1	1	2	2	n/a	1	0	n/a	0	1	2	0	1
C. middlesexensis	Claremont	0	2	2	1	1	1	1	1	1	1	n/a	1	0	n/a	0	1	2	0	1

	Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
species	location																				
C. jeffersonius	Mt. Pleasant	167.5	183	0.92	175.08	8	16.1	18.1	6.31	48.44	51.74	101.5	0.477	0.51	0.555	4.78	0.1	17.3	9.02	1.916	0.103
C. jeffersonius	Mt. Pleasant	148.1	161.2	0.92	154.5	8	14	16.3	3.03	41.28	43.4	84.72	0.487	0.512	0.526	2.33	0.06	13.6	6.41	2.122	0.092
C. jeffersonius	Mt. Pleasant	136.2	141.36	0.96	138.75	8	15.2	16.4	4.98	34.2	32.2	66.27	0.516	0.486	0.469	3.69	0.11	13.7	5.51	2.488	0.101
C. jeffersonius	Mt. Pleasant	130.5	137.37	0.95	133.9	9	12.4	15.8	5.75	37.27	37.67	74.53	0.5	0.505	0.543	n/a	n/a	11.1	6.16	1.794	0.085
C. jeffersonius	Mt. Pleasant	135.9	140.15	0.97	138	7	18.5	21.6	9.34	37.49	37.51	75.36	0.497	0.498	0.538	n/a	n/a	12.6	5.95	2.111	0.092
C. jeffersonius	Mt. Pleasant	100.3	105.66	0.95	102.93	9	9.58	10.1	5.61	29.11	24.06	53.48	0.544	0.45	0.506	n/a	n/a	8.13	5.17	1.573	0.081
C. jeffersonius	Mobjack Nursery	132.6	145.16	0.91	138.74	7	13.3	17.3	3.87	36.96	34.05	70.92	0.521	0.48	0.489	3.78	0.1	11.5	6.8	1.685	0.086
C. jeffersonius	Mobjack Nursery	134.7	140.49	0.96	137.57	8	14.4	15.5	5.96	36.32	35.42	71.66	0.507	0.494	0.51	2.05	0.06	12.2	6.21	1.961	0.09
C. jeffersonius	Mobjack Nursery	128.2	141.93	0.9	134.88	8	12.4	15.2	4.4	40.46	35.88	75.86	0.533	0.473	0.534	6.8	0.17	7.71	5.88	1.311	0.06
C. jeffersonius	Mobjack Nursery	146.5	154.7	0.95	150.55	8	13	16.7	6.02	39.24	41.38	80.79	0.486	0.512	0.522	n/a	n/a	13	6.64	1.962	0.089
C. jeffersonius	Mobjack Nursery	118.2	125.96	0.94	122.02	7	15.5	18.2	6.58	36.41	33.26	69.84	0.521	0.476	0.554	n/a	n/a	9.51	5.21	1.825	0.08
C. jeffersonius	Mobjack Nursery	101.3	101.81	0.99	101.55	7	10.3	11.9	5.16	26.92	27.2	54.07	0.498	0.503	0.531	n/a	n/a	8.54	4.48	1.906	0.084
C. madisonius	Lieutenant Run	119.2	129.71	0.92	124.33	12	8.78	8.69	3.5	37.39	28.69	66.35	0.564	0.432	0.512	4.83	0.13	10.2	5.65	1.811	0.086
C. madisonius	Lieutenant Run	84.78	91.56	0.93	88.105	14	5.58	5.36	2.81	23.15	22.08	44.15	0.524	0.5	0.482	2.56	0.11	5.66	4.54	1.247	0.067
C. madisonius	Lieutenant Run	114.4	115.52	0.99	114.97	12	9.72	8.83	2.78	37.35	29.89	67.38	0.554	0.444	0.583	6.13	0.16	7.83	5.34	1.466	0.068
C. madisonius	Lieutenant Run	89.59	87.78	1.02	88.68	14	4.58	5.08	2.4	22.42	18.04	40.09	0.559	0.45	0.457	n/a	n/a	6.77	3.37	2.009	0.076
C. madisonius	Lieutenant Run	99.44	104.9	0.95	102.13	15	5.6	7.21	2.47	28.9	23.54	52.79	0.547	0.446	0.503	n/a	n/a	7.75	5.51	1.407	0.078
C. madisonius	Lieutenant Run	103.5	108.92	0.95	106.15	13	6.17	7.63	3.8	30.92	30.63	61.9	0.5	0.495	0.568	n/a	n/a	10.7	5.57	1.926	0.104
C. madisonius	Rues Pit	131.1	139.56	0.94	135.27	14	8	7.38	2.41	40.33	39.55	79.78	0.506	0.496	0.572	10.7	0.26	8.68	5.99	1.449	0.066
C. madisonius	Rues Pit	101.3	106.03	0.96	103.64	14	4.73	5.47	2.82	33.61	27.8	61.24	0.549	0.454	0.578	7.48	0.22	8.34	4.36	1.913	0.082
C. madisonius	Rues Pit	112.4	123.78	0.91	117.96	15	6.55	6.67	3.56	40.13	32.52	72.22	0.556	0.45	0.583	10.5	0.26	9.42	5.19	1.815	0.084
C. madisonius	Rues Pit	126.8	133.08	0.95	129.92	15	6.47	7.06	2.63	39.81	39.71	78.11	0.51	0.508	0.587	n/a	n/a	12.3	5.57	2.212	0.097
C. madisonius	Rues Pit	110.2	115.25	0.96	112.69	15	5.7	6.22	2.96	35.51	30.72	66.31	0.536	0.463	0.575	n/a	n/a	7.15	4.69	1.525	0.065
C. madisonius	Rues Pit	104.8	108.8	0.96	106.77	15	5.43	6.15	2.71	33.8	28.08	62.53	0.541	0.449	0.575	n/a	n/a	8.39	4.34	1.933	0.08
C. septenarius	Lee Creek Mine	103.4	119.1	0.87	110.98	11	8.5	8.78	4.94	31.23	25.97	60.33	0.518	0.43	0.507	3.25	0.1	6.85	5.7	1.202	0.066
C. septenarius	Lee Creek Mine	67.97	70.98	0.96	69.459	7	10.6	10.1	4.24	21.95	21.62	43.41	0.506	0.498	0.612	6.01	0.27	5.6	3.59	1.56	0.082
C. septenarius	Lee Creek Mine	118.1	125.44	0.94	121.69	11	8.96	7.97	5.56	36.52	40.48	77.1	0.474	0.525	0.615	4.92	0.13	10.6	5.68	1.859	0.089
C. septenarius	Lee Creek Mine	98.22	97.62	1.01	97.92	8	8.74	10.9	5.08	26.74	24.12	50.82	0.526	0.475	0.521	n/a	n/a	5.08	4.57	1.112	0.052
C. septenarius	Lee Creek Mine	97.3	99.74	0.98	98.512	7	13	12.9	5.57	25.03	24.81	49.97	0.501	0.496	0.501	n/a	n/a	5.81	4.48	1.297	0.06
C. septenarius	Lee Creek Mine	74.57	78.3	0.95	76.412	6	11.7	13.2	4.54	20.9	20.76	41.14	0.508	0.505	0.525	n/a	n/a	6.05	3.37	1.795	0.081
C. septenarius	Sumpter County	112.7	125.04	0.9	118.68	8	11.7	13.2	6.48	38.31	37.35	74.9	0.511	0.499	0.599	4.77	0.12	11.6	5.11	2.278	0.103
C. septenarius	Sumpter County	109.3	105.61	1.04	107.44	7	14.5	13.6	5.37	33.38	32.92	65.59	0.509	0.502	0.621	6.1	0.18	12.9	4.04	3.2	0.118
C. septenarius	Sumpter County	123.3	121.04	1.02	122.15	7	13.9	17.9	5.28	37.83	36.52	73.06	0.518	0.5	0.604	5.06	0.13	12.8	6.33	2.024	0.104
C. septenarius	Sumpter County	88.61	91.46	0.97	90.024	7	10.6	12.5	5.6	27.15	25.28	51.38	0.528	0.492	0.562	n/a	n/a	8.18	5.29	1.546	0.092
C. septenarius	Sumpter County	92.52	91.27	1.01	91.893	6	10.2	13	6.37	28.62	24.99	53.31	0.537	0.469	0.584	n/a	n/a	7.51	4.41	1.703	0.081
C. septenarius	Sumpter County	78.94	80.55	0.98	79.741	8	8.85	10.3	5.38	23.53	23.06	46.51	0.506	0.496	0.577	n/a	n/a	6.52	3.76	1.734	0.083

	Character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
species	location																			
C. jeffersonius	Mt. Pleasant	0	1	2	1	1	2	1	0	0	2	0	0	0	0	2	1	1	1	1
C. jeffersonius	Mt. Pleasant	0	1	2	1	1	2	1	0	0	0	0	0	0	0	2	1	0	1	1
C. jeffersonius	Mt. Pleasant	0	2	2	1	1	2	1	0	0	1	0	0	0	0	2	1	1	1	1
C. jeffersonius	Mt. Pleasant	0	0	2	1	1	1	1	1	1	2	n/a	0	0	n/a	1	1	0	1	1
C. jeffersonius	Mt. Pleasant	0	0	2	1	1	1	1	0	0	2	n/a	0	0	n/a	2	1	0	1	1
C. jeffersonius	Mt. Pleasant	0	2	2	1	1	1	1	1	1	1	n/a	0	0	n/a	1	1	0	1	1
C. jeffersonius	Mobjack Nursery	0	2	2	1	0	2	1	0	0	1	0	0	0	0	2	2	2	0	1
C. jeffersonius	Mobjack Nursery	0	2	2	1	0	2	1	0	0	1	1	0	0	0	2	1	1	0	1
C. jeffersonius	Mobjack Nursery	0	2	2	1	0	2	1	1	0	1	1	0	0	0	2	1	1	0	1
C. jeffersonius	Mobjack Nursery	0	1	2	1	0	2	1	0	1	1	n/a	0	0	n/a	2	1	2	0	1
C. jeffersonius	Mobjack Nursery	0	2	2	1	0	2	1	1	0	1	n/a	0	0	n/a	2	1	2	0	1
C. jeffersonius	Mobjack Nursery	0	0	2	1	0	2	1	1	0	1	n/a	0	0	n/a	2	1	2	0	1
C. madisonius	Lieutenant Run	0	2	2	0	1	2	2	1	0	0	1	0	0	0	2	2	2	1	2
C. madisonius	Lieutenant Run	0	2	2	2	0	1	2	2	2	1	1	0	0	0	0	1	2	1	1
C. madisonius	Lieutenant Run	0	2	2	2	1	1	2	1	0	0	1	0	0	0	1	2	1	1	2
C. madisonius	Lieutenant Run	2	2	2	1	1	1	2	1	1	0	n/a	0	0	n/a	1	1	1	1	1
C. madisonius	Lieutenant Run	0	2	2	1	0	1	2	0	1	1	n/a	0	0	n/a	1	1	1	0	2
C. madisonius	Lieutenant Run	0	0	2	1	2	2	2	0	1	1	n/a	0	0	n/a	2	1	2	0	0
C. madisonius	Rues Pit	0	2	2	2	1	1	2	0	0	0	1	0	1	0	1	1	1	2	1
C. madisonius	Rues Pit	0	2	2	1	0	2	2	0	0	0	1	0	1	0	1	1	1	2	1
C. madisonius	Rues Pit	0	2	2	0	1	2	2	0	1	0	0	0	0	0	2	1	2	2	1
C. madisonius	Rues Pit	0	0	2	1	0	2	2	0	0	0	n/a	0	0	n/a	2	1	2	2	1
C. madisonius	Rues Pit	0	2	2	1	1	0	2	0	0	1	n/a	0	0	n/a	1	1	1	2	1
C. madisonius	Rues Pit	0	2	2	1	0	1	2	0	0	1	n/a	0	0	n/a	1	1	2	2	1
C. septenarius	Lee Creek Mine	0	2	2	0	2	1	1	1	1	2	1	0	0	0	0	1	1	0	1
C. septenarius	Lee Creek Mine	0	0	2	0	0	1	1	2	2	2	1	0	1	0	0	2	2	1	1
C. septenarius	Lee Creek Mine	0	1	2	2	0	2	2	1	1	1	1	0	0	0	2	1	2	1	2
C. septenarius	Lee Creek Mine	1	2	2	1	0	0	2	2	2	2	n/a	0	0	n/a	0	1	0	1	1
C. septenarius	Lee Creek Mine	0	0	2	0	1	1	2	1	2	2	n/a	0	1	n/a	0	2	1	2	1
C. septenarius	Lee Creek Mine	0	0	2	1	0	1	1	2	2	2	n/a	0	0	n/a	0	1	0	2	1
C. septenarius	Sumpter County	0	2	2	1	1	2	2	2	0	2	0	0	0	0	2	2	0	0	1
C. septenarius	Sumpter County	2	0	2	2	0	2	2	2	0	2	1	0	0	0	2	2	2	1	1
C. septenarius	Sumpter County	2	2	2	1	0	2	2	2	2	2	0	0	0	0	2	1	2	1	1
C. septenarius	Sumpter County	0	2	2	1	1	2	2	2	2	2	n/a	0	0	n/a	1	2	0	2	1
C. septenarius	Sumpter County	2	2	2	1	1	1	1	2	2	2	n/a	0	0	n/a	0	1	1	1	1
C. septenarius	Sumpter County	0	0	2	1	0	1	1	2	1	2	n/a	0	0	n/a	1	1	0	1	1

Appendix D: List of synapomorphies and autapomorphies

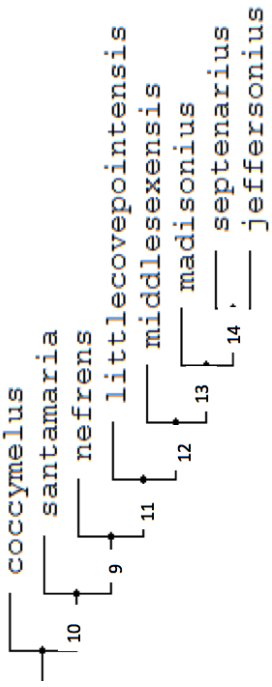
C. coccymelus has no autapomorphies because it is the outgroup. The nudes to which synapomorphies correspond are depicted in the image of the phylogenetic tree.

Autapomorphies

characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
C. nefrens	x	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x				x		x	x					x		
C. littlecovepointensis	x	x					x	x		x			x										x			x	x				x			x	x			
C. santamaria				x	x									x												x	x							x					
C. middlesexensis	x	x	x	x	x	x							x				x			x							x			x				x		x		
C. jeffersonius	x	x	x		x	x	x	x	x	x	x			x	x	x	x	x	x	x				x				x			x		x	x		x	x	
C. madisonius																		x					x	x					x						x	x		
C. septenarius	x	x	x					x					x			x				x	x						x	x										

Synapomorphies

characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Node 9											x	x				x		x	x	x			x		x				x	x				x					
Node 10																														x									
Node 11															x															x		x					x	x	
Node 12														x	x													x				x		x	x		x	x	
Node 13				x	x	x	x				x	x		x	x				x		x								x										
Node 14				x					x	x			x						x		x			x						x	x		x	x			x	x	



Appendix E: Landmark data

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
sample1-internal1	-0.0016	0.075396	0.033887	-0.0346	-0.0122	-0.01586	0.002579	-0.00594	0.024181	0.011832
sample1-internal2	-0.01025	-0.04489	0.026775	-0.00594	0.010198	0.004348	0.020659	0.010044	0.019574	-0.01364
sample1-internal3	-0.02012	0.020901	0.048489	-0.0035	0.056982	-0.02165	0.022619	0.017859	0.004054	-0.01705
sample1-internal4	-0.01365	0.020005	0.022672	-0.00887	0.04266	0.027952	0.011188	0.012968	-0.0043	0.010012
sample1-internal5	-0.0556	-0.03301	-0.02282	0.052705	0.018598	-0.00447	0.014911	-0.0226	0.008128	-0.01973
sample1-internal6	-0.05399	-0.04015	0.038006	0.023313	-0.01632	-0.00223	-0.00106	-0.02008	-0.01284	0.009278
sample1-internal7	-0.07174	0.034936	0.056635	0.056507	-0.01805	-0.0049	0.003463	0.00178	0.002169	0.007529
sample1-internal8	0.049137	0.029569	-0.05093	-0.01641	-0.0084	-0.00191	0.005012	0.001805	-0.00167	-0.01514
sample1-internal9	-0.03249	0.035036	-0.00598	-0.01364	-0.03491	0.055476	-0.02794	0.017918	-0.00955	0.006349
sample1-internal10	-0.01107	0.098984	-0.00084	0.0435	-0.02304	-0.04332	-0.01927	-0.00246	0.006113	0.000972
sample1-internal11	-0.04763	-0.01177	-0.07387	0.034439	0.015964	0.007558	0.015024	-0.01863	-0.00604	-0.00035
sample1-internal12	-0.04462	0.030132	-0.02582	0.020702	-0.00559	0.006395	0.017631	0.005527	-0.0129	0.003298
sample2_internal3	0.047709	0.0824	0.069197	-0.01841	0.004524	0.076185	-0.00806	-0.03329	0.017701	-0.02638
sample2_internal1	0.05802	-0.00541	0.00236	-0.00973	0.020799	0.009137	0.002776	-0.00356	0.006615	0.01055
sample2_internal2	-0.00469	-0.02501	0.010718	-0.01118	0.031558	-0.00801	0.013295	-0.00838	-0.00112	0.012609
sample2_internal4	-0.01994	-0.04084	0.047771	-0.02007	0.013059	0.009806	-0.00024	-0.00813	0.00691	0.005545
sample2_internal5	0.06012	-0.03902	0.050714	0.041899	-0.02134	0.008375	0.006468	0.016554	0.020691	0.008585
sample2_internal6	0.054623	-0.00438	0.015247	0.004237	-0.0383	0.013526	0.003244	0.011888	-0.00525	0.005531
sample2_internal7	-0.03107	-0.05526	0.000865	0.002173	-0.00413	0.003163	0.023802	-0.00635	-0.00011	-0.00511
sample2_internal8	-0.02834	-0.05474	0.038968	0.013722	-0.01615	-0.01166	-0.00264	0.003663	0.013131	-0.00473
sample2_internal9	0.042862	0.004679	0.000826	0.011478	-0.05346	0.018918	0.009561	0.025321	0.00568	0.010367
sample2_internal10	-0.0796	-0.02132	0.03947	0.04961	-0.01343	0.024161	-0.02469	0.000226	-0.00625	-0.00564
sample2_internal11	-0.06865	-0.0119	-0.06911	0.02987	-0.00018	0.032144	0.000181	-0.0036	0.013751	0.006376
sample2_internal12	-0.07668	0.027397	-0.05909	0.029631	0.002091	0.00608	-0.01827	-0.00338	0.015794	0.010544
sample2_internal13	-0.08404	0.009936	-0.033	0.008769	-0.00326	0.000834	0.011602	-0.00641	0.010498	0.012288
sample3_internal1	0.040431	0.011609	0.047233	0.038221	0.019122	0.00846	-0.01229	0.002476	-0.00013	-0.00187
sample3_internal2	0.037894	0.014558	-0.00672	0.021609	-0.01627	-0.03923	-0.03115	-0.02343	-0.01118	0.001165
sample3_internal3	0.064312	0.013981	-0.04263	0.025406	-0.00994	-0.00856	-0.00078	0.00441	-0.00055	0.000141
sample3_internal4	-0.02123	-0.03273	-0.01551	0.015382	-0.00549	0.006761	-0.0039	0.007197	0.000675	-0.01008
sample3_internal5	0.00332	-0.03466	-0.01443	0.036024	0.025574	-0.00057	-0.01124	-0.01184	0.000165	-0.0036
sample3_internal6	0.066243	-0.01795	-0.02808	-0.00274	-0.02978	-0.00612	0.006901	-0.00709	0.000886	0.01205
sample3_internal7	0.050664	-0.00088	0.013631	-0.01311	-0.03277	-0.01956	-0.01178	-0.00304	-0.00652	-0.00082
sample3_internal8	-0.02832	-0.0492	0.014489	0.02165	-0.03295	-0.02455	0.003737	0.000359	0.0036	0.000972
sample3_internal9	0.031821	-0.00299	-0.00455	0.018111	0.010104	-0.01046	0.020714	0.008146	-0.00628	-0.00346
sample3_internal10	-0.01958	-0.04565	0.01581	0.005279	-0.01193	-0.00175	-0.01702	0.002255	0.016441	-0.00367
sample3_internal11	0.085307	-0.0589	-0.00109	0.027577	0.006865	0.006342	-0.00804	-0.00195	0.001601	-0.01386
sample3_internal12	-0.00749	-0.00699	-0.04466	-0.02136	-0.00364	0.004562	0.022775	-0.00197	0.007865	-0.00431
sample3_internal13	0.0455	0.037523	-0.00781	0.011011	-0.00094	0.004125	0.002098	0.002994	-0.00395	0.005429
sample3_internal14	-0.03765	0.000723	-0.02596	-0.02528	-0.02262	0.001518	0.024614	0.002299	0.005398	-0.01133
sample3_internal15	0.054995	-0.00969	-0.06433	-0.00755	-0.0109	0.019815	-0.00912	-0.01957	0.007169	-9.18E-05
sample3_internal16	-0.02204	-0.00412	0.030404	0.01026	0.019663	0.015327	0.011747	0.013663	-0.02476	-0.0069
sample3_internal17	0.025764	-0.05914	0.003888	-0.00119	-0.02444	-0.02526	0.002754	-0.00456	-9.12E-05	-0.00956
sample3_internal18	0.003937	-0.02227	0.001081	-0.00395	0.007471	-0.00642	0.003948	0.004186	-0.00804	0.005636
sample3_internal19	0.008492	-0.04977	0.004474	-0.02683	-0.00291	0.000432	0.001076	-0.00129	-0.02025	0.006406
sample3_internal20	-0.007	-0.02874	0.02074	0.001608	0.025664	-0.0071	-0.02195	0.013637	-0.00035	0.014395

	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19	PC20
sample1-internal1	-0.00342	0.011664	-0.00734	-0.00584	-0.0013	-9.95E-05	-0.00134	2.07E-08	8.72E-09	8.54E-09
sample1-internal2	0.000974	0.006097	-0.00253	0.000842	-0.00087	-0.00203	0.001925	-2.64E-10	-3.61E-08	-1.66E-08
sample1-internal3	0.003426	-0.00497	0.000669	0.001717	0.002248	0.006054	-0.00032	-1.39E-08	-3.19E-08	-1.03E-08
sample1-internal4	-0.01337	0.005458	0.007332	0.002403	0.002529	0.002618	-0.0009	2.86E-09	-1.49E-08	-2.32E-08
sample1-internal5	0.004219	-0.00934	-0.0047	0.00631	-0.00308	-0.0025	0.000683	2.35E-08	1.69E-09	-1.48E-08
sample1-internal6	-0.00667	0.016159	0.00139	-0.00134	0.001521	0.001644	0.000715	-1.14E-09	7.63E-10	1.97E-08
sample1-internal7	0.008862	0.000939	0.005737	0.002178	0.002096	0.003644	0.000564	-2.18E-08	-4.48E-09	-3.34E-08
sample1-internal8	-0.00698	0.01507	-0.01093	0.003926	-0.00103	9.88E-05	-0.00109	-2.82E-08	-3.81E-08	-1.29E-09
sample1-internal9	-0.01394	-0.00389	-0.00663	0.003382	-0.00487	-0.00072	0.001049	-1.61E-08	-4.34E-09	-8.97E-09
sample1-internal10	0.00853	-0.00709	-0.00231	0.000208	-0.00143	0.003611	0.000345	-2.09E-08	-7.62E-09	1.42E-08
sample1-internal11	0.008137	-0.00701	-0.00021	0.00528	-0.00214	0.001856	-0.00264	8.89E-09	5.24E-09	-2.72E-09
sample1-internal12	0.019089	-0.0027	0.001096	-0.00203	0.001964	-0.00098	0.000795	-1.15E-08	1.35E-08	-8.90E-09
sample2_internal3	0.017173	0.005798	-0.00059	0.002321	0.000111	0.001146	-0.00056	-1.28E-08	4.91E-09	1.89E-09
sample2_internal1	-0.00695	0.00503	0.000566	0.00367	-0.00389	-0.00141	-0.00021	-2.10E-08	-2.41E-09	2.33E-08
sample2_internal2	0.004537	-0.00238	-0.00281	0.001831	0.004995	0.00056	-0.00025	-6.61E-10	7.77E-09	3.42E-08
sample2_internal4	-0.0004	-0.01076	0.003163	0.00337	0.001154	0.000524	-0.00116	-2.72E-09	-6.88E-09	5.47E-09
sample2_internal5	-0.00019	-0.00332	-0.00079	-0.00102	-0.00337	0.002697	-0.00168	7.27E-09	2.01E-08	-1.56E-08
sample2_internal6	0.006145	0.002862	0.007112	0.00268	-0.00248	-0.00039	0.000194	-7.85E-09	-1.88E-08	-7.11E-09
sample2_internal7	-0.01419	0.000836	-0.0048	-9.36E-05	-0.00043	0.000875	-0.00247	-9.75E-09	3.31E-08	-1.53E-08
sample2_internal8	-0.0007	-0.00138	0.002091	-0.00331	0.00097	0.000153	-0.00071	5.78E-09	-1.45E-08	4.95E-08
sample2_internal9	0.002644	-0.0022	0.006237	0.001652	0.000604	0.00148	0.000134	1.05E-09	-1.15E-08	6.24E-09
sample2_internal10	0.004577	-0.00305	-0.01054	-0.004	0.000352	0.000263	0.000893	2.71E-08	-7.99E-09	6.23E-09
sample2_internal11	-0.00494	0.00794	0.003285	-0.00442	0.000128	0.002963	0.000713	-9.77E-09	7.15E-09	2.47E-09
sample2_internal12	0.014183	0.00617	0.002164	-0.00094	-0.00239	-0.00042	-0.00096	4.93E-09	5.53E-09	1.02E-08
sample2_internal13	-0.00563	-0.00823	-0.00409	-0.00219	0.000304	0.002651	0.000186	-2.45E-08	-7.71E-09	-1.60E-09
sample3_internal1	-0.00761	-0.00362	0.00629	0.002421	0.000914	-0.00113	-9.51E-05	-2.33E-09	1.21E-08	1.50E-08
sample3_internal2	-0.00012	0.003267	-0.00076	0.005401	0.002643	-0.00152	-0.00053	-2.06E-09	6.64E-09	-3.04E-08
sample3_internal3	0.004591	-0.00032	7.76E-05	0.000151	-0.00099	0.001247	0.001966	2.41E-08	2.42E-08	-3.16E-08
sample3_internal4	-0.00233	0.007137	0.006063	0.006884	-0.00171	-0.00442	-0.00092	-2.03E-08	-2.50E-09	-1.40E-08
sample3_internal5	-0.00212	0.011235	-0.00037	-0.00415	0.002719	-0.00369	-0.00043	9.26E-10	-3.16E-08	-1.18E-08
sample3_internal6	0.006769	-0.00073	-3.18E-06	0.000954	-0.00093	0.001964	-0.00072	-2.08E-08	-1.86E-09	-1.89E-08
sample3_internal7	0.001637	0.008216	-0.00395	-0.00069	0.003022	-9.10E-05	-0.0008	-6.35E-09	-4.88E-08	-1.81E-08
sample3_internal8	-0.00032	0.007205	0.000491	0.00299	8.44E-05	0.000408	-0.00029	5.61E-09	4.61E-08	4.94E-09
sample3_internal9	-0.00134	0.00468	0.003623	-0.00092	-0.00091	-0.0008	0.000695	1.84E-08	3.07E-08	3.41E-08
sample3_internal10	-0.00283	0.004575	-0.00147	0.001566	0.001845	-0.00414	0.000222	-2.30E-08	-1.52E-08	-1.67E-08
sample3_internal11	-0.00246	0.00204	0.001504	-0.00133	-0.00404	0.005128	-4.54E-05	-6.23E-10	5.89E-09	1.06E-08
sample3_internal12	0.005518	0.003981	-0.00069	-0.00463	-0.00094	-0.00206	0.000802	-9.28E-09	4.06E-08	-2.08E-08
sample3_internal13	-0.00876	-0.00302	0.003229	0.001674	-0.00314	-0.00175	0.001096	-1.70E-08	2.17E-08	2.62E-08
sample3_internal14	0.003482	-0.00474	-0.00158	0.000139	0.002084	-0.00034	0.001414	2.22E-09	-1.59E-08	3.34E-08
sample3_internal15	-0.00152	-0.00527	0.003756	-0.00062	0.000482	0.00108	0.000566	8.60E-09	-3.91E-08	3.22E-08
sample3_internal16	-0.00155	0.000299	-0.00492	-0.00034	-0.00163	-0.00032	0.001847	1.95E-08	8.11E-09	1.57E-08
sample3_internal17	-0.00539	-0.00352	-0.00474	-0.00323	-0.00085	0.002234	-0.00027	-1.74E-08	-4.24E-08	3.25E-08
sample3_internal18	0.002066	0.001776	0.001004	-0.00283	0.000392	-0.00167	0.000518	-4.33E-08	3.07E-08	-1.18E-08
sample3_internal19	0.015378	0.000112	-0.01263	0.00295	-0.00029	0.001401	0.000867	-2.11E-08	-1.21E-08	1.34E-08
sample3_internal20	0.013974	0.004293	-0.00473	-0.00157	-0.00835	-0.00391	0.000248	1.66E-08	-8.57E-09	7.37E-09

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
sample4_internal1	-0.01987	-0.0002	0.023466	-0.03711	0.014824	-7.72E-05	0.003143	-0.00543	-0.01814	0.000467
sample4_internal2	0.046295	0.026935	-0.01255	0.0038	0.016024	-0.00313	0.013576	-0.01477	0.013592	0.01034
sample4_internal3	0.007363	0.000318	0.011172	-0.01397	0.010736	-0.01066	-0.00112	0.024523	0.007481	-0.01968
sample4_internal4	0.00506	-0.03828	0.00565	0.003299	0.018589	0.001394	0.009184	-0.00034	-0.01647	0.003046
sample4_internal5	-0.0534	0.03043	-0.00171	-0.00331	-0.00549	-0.00375	0.000545	0.002675	-0.01806	-0.01248
sample4_internal6	0.058499	0.001772	-0.00714	0.010137	0.012618	0.015057	0.004808	0.002434	-0.01638	-0.00765
sample4_internal7	0.038675	0.021478	-0.00753	-0.00242	-0.03222	-0.00489	0.010675	0.003359	-0.00491	-0.00572
sample5_internal1	-0.02531	0.001187	-0.03107	-0.04546	-0.01813	-0.00154	0.003239	-0.00095	0.00629	0.001058
sample5_internal2	0.01974	-0.05306	-0.04704	-0.03352	0.007179	0.003675	-0.06171	0.016552	0.003509	-0.01803
sample5_internal3	-0.031	-0.01513	0.006135	-0.02854	-0.02184	-0.01604	0.017429	-0.00639	0.004775	-0.00195
sample5_internal4	0.01343	0.013964	-0.03375	-0.00357	0.029582	-0.03356	-0.01983	0.003383	-0.00104	-0.00977
sample5_internal5	-1.56E-05	0.042823	0.002956	-0.01649	-0.03576	-0.01424	0.002853	-0.00438	-0.00422	0.00149
sample5_internal6	-0.02304	-0.00608	0.00053	-0.00327	0.001086	0.004249	0.001878	0.003544	0.000794	0.001163
sample5_internal7	-0.00392	-0.00681	0.006712	-0.02211	-0.00855	-0.01009	-0.00826	0.006449	0.000706	-0.00763
sample5_internal8	0.034566	0.008854	-0.02875	-0.00546	0.017064	3.79E-05	0.018135	-0.00539	-0.00085	0.010229
sample5_internal9	-0.0262	-0.01691	0.047224	-0.05708	-0.01734	1.43E-06	-0.03348	-0.0256	-0.005	0.004597
sample5_internal10	0.044577	-0.02406	0.011019	-0.02028	-0.00694	0.004616	0.009496	-0.00481	0.004788	0.005816
sample5_internal11	-0.01134	-0.00386	-0.00933	-0.03753	0.000228	-0.00354	0.006113	0.01522	0.018914	0.001157
sample5_internal12	0.060773	-0.02856	0.016497	0.003274	0.026382	0.00125	0.002104	-0.01635	0.001951	0.005346
sample5_internal13	-0.00024	-0.02073	0.030058	-0.01122	0.013363	-0.01568	-0.00867	0.006018	0.00771	0.019727
sample6_internal1	0.03871	0.014877	-0.00029	-0.00428	0.009648	0.012328	0.00145	-0.01333	-0.01155	0.019078
sample6_internal2	0.006032	-0.01193	0.000977	-0.01552	0.020153	-0.01282	-0.03132	-0.00159	0.005415	0.013765
sample6_internal3	0.057484	0.021748	-0.01295	0.026488	0.037831	0.002081	0.00882	-0.00317	0.00738	0.000933
sample6_internal4	0.023496	0.047908	0.036716	0.009997	0.013418	-0.01103	0.010032	-0.00131	0.004567	0.00447
sample6_internal5	0.05945	0.014405	-0.00026	0.020973	-0.00563	0.00854	0.022858	0.003494	-0.01769	0.008689
sample6_internal6	-0.02807	0.041342	-0.0307	-0.0165	0.05494	-0.00726	-0.01692	0.018838	-0.00143	0.015265
sample6_internal7	-0.04346	0.039748	0.024714	-0.00075	0.010734	-0.00572	0.001166	0.014546	0.002896	0.00064
sample6_internal8	0.002349	0.009078	-0.02239	-0.01759	0.01187	-0.01074	-0.0142	0.005476	-0.00215	0.003622
sample6_internal9	-0.02584	-0.00661	-0.00604	-0.03517	-0.01297	-0.00264	0.025729	-0.00802	-0.01598	-0.00697
sample6_internal10	-0.0607	0.031468	0.029621	-0.04145	0.000788	-0.01516	0.006405	-0.02761	-0.00798	-0.00504
sample6_internal11	-0.03416	0.019677	-0.00322	-0.03452	0.017118	-0.00948	-0.01282	-0.00139	0.000709	-0.01052
sample6_internal12	-0.04956	0.011043	-0.00817	0.019827	-0.00712	0.014439	-0.00882	0.00105	0.002971	0.006737
sample6_internal13	-0.02331	0.002912	-0.0199	-0.00454	0.000138	0.025006	-0.01949	0.007427	-0.0146	-0.0017
sample6_internal14	-0.00573	-0.01908	-0.01019	-0.01141	0.000784	0.017669	-0.0119	0.010204	-0.00697	0.005105
sample6_internal15	0.009488	0.057616	0.026306	0.042688	-0.01724	-0.01908	-0.00911	0.008001	-0.01482	-0.01497
sample6_internal16	0.03375	0.039568	-0.02456	0.009164	0.009696	-0.00768	-0.00727	-0.00165	0.003902	-0.01909
sample6_internal17	-0.02665	0.015757	-0.01934	-0.03692	-0.02315	0.000658	0.030308	0.019642	0.003208	-0.00209

	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19	PC20
sample4_internal1	0.003295	0.00394	0.001675	0.00222	-0.00203	-0.00051	-0.00135	-8.10E-10	4.93E-08	-4.69E-10
sample4_internal2	-0.00587	-0.01222	0.00269	0.002207	-0.00334	-0.00262	0.000509	-7.33E-09	-2.28E-08	-1.59E-08
sample4_internal3	0.007322	-0.00789	0.001839	-0.00413	-0.00281	-0.0034	-0.00172	2.34E-09	2.65E-08	1.71E-08
sample4_internal4	-0.00546	0.001163	0.002277	0.000509	-0.00459	-0.00018	0.000348	-1.69E-08	-2.25E-08	-9.40E-10
sample4_internal5	-0.00184	-0.00337	-6.31E-05	0.000839	0.001992	-0.00027	-0.00033	-2.10E-08	-1.07E-09	1.17E-08
sample4_internal6	-0.00782	-0.00667	0.002531	-0.00766	0.00271	0.001935	-0.00129	-2.88E-09	-1.09E-08	-5.02E-08
sample4_internal7	0.000503	-0.00071	0.000312	-0.00145	0.001575	-0.0017	-0.00056	1.45E-08	-2.46E-08	-1.50E-08
sample5_internal1	-0.00904	-0.0077	0.001731	-0.00203	0.000755	0.001975	0.001284	8.86E-09	-1.62E-08	1.65E-08
sample5_internal2	0.005489	-0.00265	-0.0008	0.001615	0.001778	0.006834	-9.23E-05	3.00E-08	4.84E-08	4.39E-09
sample5_internal3	-0.01015	0.002565	0.003861	0.006719	-0.00251	-0.00027	0.000761	2.38E-08	-2.11E-08	-2.91E-08
sample5_internal4	-0.00142	0.006905	0.003115	0.00155	-0.00133	7.10E-05	0.001043	-1.95E-08	-1.29E-08	-2.50E-08
sample5_internal5	-0.01013	-0.00253	0.000704	0.004302	0.003011	-0.00037	0.000106	2.25E-08	2.91E-08	-8.03E-09
sample5_internal6	-0.01373	-0.00213	0.004491	-0.0009	0.002659	-0.00221	0.000515	1.28E-08	5.75E-09	-1.37E-08
sample5_internal7	0.004438	-0.00136	0.004983	0.005726	0.004136	-0.00266	-0.00064	1.23E-08	4.51E-08	1.97E-08
sample5_internal8	-0.00538	-0.01442	-0.00777	0.001343	-0.00181	-0.00059	-0.00109	-2.91E-09	1.58E-08	-1.07E-08
sample5_internal9	-0.00288	-0.00512	0.004061	-0.00211	-0.00277	0.002374	0.001023	-1.03E-08	1.75E-08	-2.33E-08
sample5_internal10	0.005439	-0.00238	-0.00531	0.0043	0.00103	-0.00136	0.001874	1.32E-08	2.99E-08	-5.20E-09
sample5_internal11	0.003048	-0.00108	-0.00387	0.004845	0.00512	-0.00081	-0.00051	-2.96E-08	1.47E-09	-2.76E-08
sample5_internal12	0.000392	-0.0069	0.004003	-0.00192	-0.00157	0.000961	0.001581	1.97E-08	-4.32E-09	-9.75E-09
sample5_internal13	0.008879	-0.00648	-0.00254	-0.00075	0.006692	0.000755	0.000424	-2.44E-09	-1.88E-08	-1.47E-08
sample6_internal1	1.47E-06	-0.00468	-0.00313	-0.00074	0.002764	-0.00171	-0.00044	1.41E-08	1.03E-09	4.27E-08
sample6_internal2	-0.00399	-0.00325	-0.00044	-0.015	-0.00237	-0.00237	-0.00115	-6.55E-11	2.23E-09	-5.75E-09
sample6_internal3	-0.00858	0.010506	-0.00738	-0.0052	0.008059	0.001801	0.002034	-8.05E-09	3.18E-08	-1.78E-09
sample6_internal4	0.014717	0.001341	-0.00083	0.00093	-0.00047	-0.00358	4.51E-05	2.46E-08	-4.95E-09	1.45E-08
sample6_internal5	0.005542	0.006451	-0.00427	0.001357	0.001995	0.001172	-0.00127	2.92E-08	7.64E-09	1.56E-08
sample6_internal6	-0.00053	0.010957	0.000792	0.006759	-0.00412	0.004451	-0.00021	1.57E-08	-2.39E-08	8.04E-09
sample6_internal7	-0.00822	-0.00472	-0.00436	-0.0038	-0.00346	-0.00138	0.000706	-2.92E-08	6.65E-11	-3.02E-08
sample6_internal8	0.010932	-0.00042	0.012592	0.004457	0.000839	-0.00161	0.000324	3.39E-09	-8.30E-09	1.23E-08
sample6_internal9	0.016932	0.003241	0.016132	-0.01099	-0.00211	0.001335	-0.00022	-1.74E-08	-3.16E-08	-1.10E-08
sample6_internal10	-0.00569	0.004947	-0.00047	-0.002	-0.00413	0.001537	0.000156	2.34E-08	1.98E-08	-5.54E-09
sample6_internal11	-0.00619	-0.00345	-0.0009	0.005772	0.001814	-0.00106	-5.71E-05	7.65E-09	-1.84E-08	2.49E-08
sample6_internal12	-0.01559	0.001934	0.008578	0.000628	0.004333	-0.00197	-0.00111	2.76E-08	-2.44E-09	3.17E-08
sample6_internal13	0.00739	-0.00562	-0.00675	-0.00403	0.004084	-0.00381	-0.0017	-2.79E-09	-3.57E-08	-2.99E-08
sample6_internal14	0.002971	-0.00096	0.001771	0.000299	0.004183	-0.00172	0.001099	2.18E-09	3.06E-09	-5.26E-09
sample6_internal15	-0.01433	-0.00649	-0.00222	-0.00073	-0.00225	9.62E-05	-0.00031	3.01E-09	-4.69E-09	1.64E-08
sample6_internal16	-0.00463	-0.00122	0.004789	-0.00913	0.001849	-0.00271	0.000712	4.70E-09	2.12E-08	1.65E-08
sample6_internal17	0.00201	0.005169	-0.00461	-0.00521	-0.00179	0.001632	-0.00054	4.39E-08	1.92E-08	1.33E-08